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NATURAL HISTORY

STUDIES ON THE STRUCTURE AND TAXONOMY OF *BULINUS JOUSSEAUMEI* (DAUTZENBERG)

C. A. WRIGHT

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BY

C. A. WRIGHT

Pp. 1–28 ; *Plates* 1–2 ; 41 *Text-figures*

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STUDIES ON THE STRUCTURE AND TAXONOMY OF *BULINUS JOUSSEAUMEI* (DAUTZENBERG)

By C. A. WRIGHT

SYNOPSIS

Many recent workers on the freshwater mollusca of Africa have tended to present synonymies based more on the literature and on personal opinions than on a study of the animals themselves. This is particularly true of those gastropods of medical importance which act as intermediate hosts for flukes parasitizing human beings. This paper is an attempt to establish the relationships of one such snail.

HISTORICAL

DAUTZENBERG (1890) described *Bulinus jousseaumei* as a member of the genus *Isidora* and stated that it belonged to the *I. contorta* group with a strong affinity to *I. natalensis*. Pilsbry & Bequaert (1927) list *B. jousseaumei* in the sub-genus *Bulinus* s. str. and Amberson and Schwarz (1953) place it in the synonomy of *B. truncatus*. I have shown that both on conchological and anatomical grounds the species is properly placed in the sub-genus *Physopsis* (Wright 1956). Smithers (1956) has shown that in parts of the Gambia Protectorate this snail is an important vector of the human blood-fluke, *Schistosoma haematobium*. From personal observations I am sure that it is also the vector implicated in the Casamance Province of Senegal by Deschiens (1951) under the name *Bulinus trigonus*, a species characteristic of some lakes in East Africa.

MATERIAL AND METHODS

The material of *B. jousseaumei* from the Gambia and Senegal used in this work was collected personally, in collaboration with S. R. Smithers. Material from other localities has mostly been seen in the collection of the British Museum (Natural History) or has been sent to me by other workers.

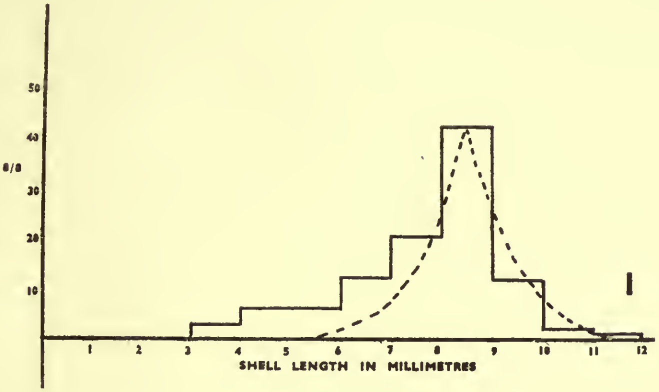
Shell measurements were made with an eyepiece micrometer in a binocular dissecting microscope, the shells were held steady in a horizontal position by means of a piece of plasticine on the microscope stage. Radula preparations were made following the rapid methods recommended by Meeuse (1950).

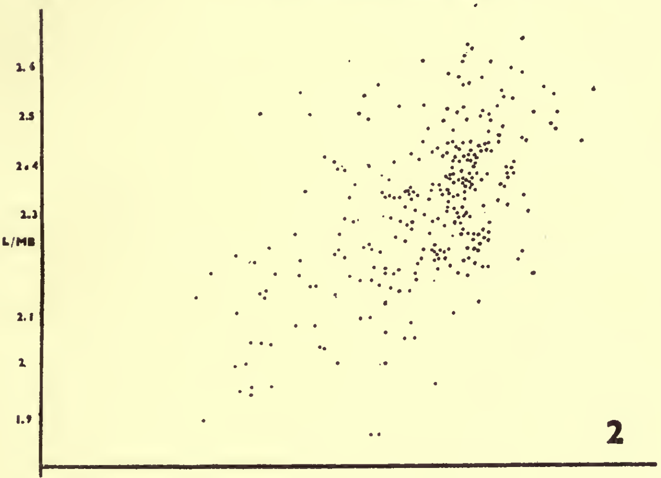
THE SHELL

The original description of the shell by Dautzenberg is very adequate and my redescription (Wright, 1956) adds little to the original, apart from noting a further colour variation from light yellowish-straw to dark reddish-brown, and amplifying the details of the ornamentation. Since reference will be made later to the sculpture my previous observations are repeated here. There is a regular punctate pattern on the nuclear whorl and the rest of the shell is covered with fine growth lines superimposed on which is a delicate pattern of short, wavy, vertical lines. It is surprising that Dautzenberg, who must have been acquainted with *Physopsis*, was so definite about the affinities of *B. jousseaumei* in spite of his mention of the twisted base of the columella in his description.

One of the greatest difficulties in the description of gastropods is the definition of size. The old workers when describing a new species usually gave the dimensions of the specimen (often the largest) which they had selected as the holotype. Rarely, they gave the dimensions of the largest and the smallest specimens available to them. The dangers of this approach to the problem in an animal which grows steadily without a well-defined adult phase are obvious. Size ranges are valueless since they give no idea of distribution, and ranges given with a mean and standard deviation are not of much use unless the growth stages represented in the sample are known. The ratios of certain measurements of the shell are of more value but these may vary with shell length. For instance Peters (1938) has shown that the ratio shell length/aperture length increases with shell length in *Lymnaea palustris*. Hubendick (1951) using smaller samples suggests that there is no significant change in the ratio aperture length/shell length × 100 in *Lymnaea peregra*.

In order to investigate the relationships of *B. jousseaumei* it has been found necessary to analyse the size composition of various samples. The largest of these samples was collected at a washing place in the Simoto Bolon near the village of Diabugu Basilla, Upper River Division, Gambia on the 4th March, 1955. Two-hundred and thirty-eight shells were measured and spirit material dissected to try to determine an approximate correlation between shell size and the attainment of the "adult" condition. The results obtained from a study of this sample appear to be characteristic for the other samples collected in the Gambia at the same time. The time of year at which a sample is collected is of great importance since it is almost certain that the population early in the wet season contains a much higher proportion of juveniles than it would some months after the end of the rains, the time when the material under consideration was collected. Text-fig. 1 is a size frequency histogram of this sample, based on shell length. It is obvious that the greatest frequency occurs in the 8·0–9·0 mm. shell length group and the mode of the graph is at the 8·5 mm. level. The graph is, however, asymmetrical due to an overweighting of the lower size groups, the mean shell length of the sample is therefore less than the modal length. The graph does not provide any indication of whether the mode is due to large numbers of adults or juveniles and this can only be determined by anatomical study. It will be shown later that it is in the size group 6·0–7·0 mm. shell length that the accessory reproductive glands reach a fully functional stage of their development and this is taken as the beginning of the adult phase of life. If the curve showing distribution on the upper side of the mode in Text-fig. 1 is drawn and its mirror image is reproduced on the low side a normal distribution curve is formed, the lower end of which coincides well with the known onset of the adult phase. If the frequency distribution is plotted on arithmetical probability paper following the





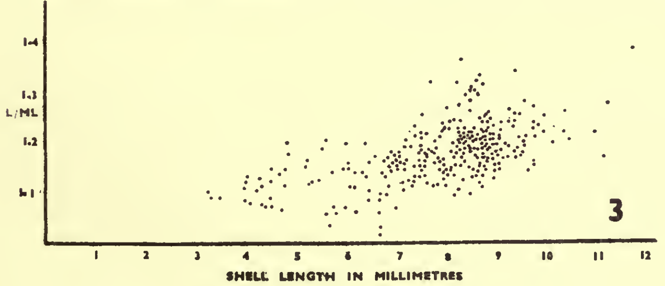


FIG. 1. Size-frequency histogram for a population of *B. jousseaumei* from the Gambia.

FIG. 2. Graph of ratio shell length/aperture width against shell length for Gambian population of *B. jousseaumei*.

FIG. 3. Graph of ratio shell length/aperture length against shell length for the same population.

method of Harding (1949) a curve is obtained which appears to be too complex to be analysed by the usual methods. This may in part be due to faulty sampling but is also undoubtedly caused by the complicated structure of a population of fresh water snails. There may be present the representatives of several successive generations, a few senescent survivors of previous generations, the adults of the present and the progeny of these adults. If the breeding season is continuous then a smooth curve might be expected but there is reason to believe that breeding is somewhat spasmodic in the bulinids and this might help to account for the complex composition of the population. Since the anatomical findings confirm that the mode of the histogram in Text-fig. 1 is in fact the mean of the adult part of the population it seems justifiable to accept 8·5 mm. as the mean shell length of the adults in this sample. An indication of the proportion of juveniles in the whole sample is given by the index of skewness, (mean-mode)/standard deviation. Having obtained a rough mean length for the adults in the population the adult means for the other dimensions may be calculated by increasing the population mean by the same percentage as that by which the mean population length differs from the adult mean length. The following table gives the mean shell dimensions of the population in millimetres and their standard deviations together with the approximate adult dimensions and the maximum sizes observed.

	Length		Max. diam.		Aperture length		Aperture width	
	Mean	S. D.	Mean	S. D.	Mean	S. D.	Mean	S. D.
Whole population	7·84	±1·52	6·00	±1·12	6·65	±1·03	3·37	±0·66
Adults	8·5	—	6·50	—	7·2	—	3·65	—
Maximum	11·8		8·0		9·0		4·5	

Passing from the absolute dimensions of the shells to the ratios of some of these dimensions to one another, one is faced with a number of these proportions from which to choose the most useful. Hubendick (1951) pointed out that the selection of measurements in any particular case should be made with advance knowledge of the variation to be studied. In this study of *B. jousseaumei* the object of interest is not so much phenotypic or genotypic variation as changes in form during growth. With this in mind the two ratios chosen are those of shell length/aperture length (l/ml) and shell length/aperture width (l/mb). The first of these in this type of shell gives an indication of the exsertion of the spire for if the spire is strongly depressed the ratio will approach unity and will increase with the exsertion of the upper whorls, or, more properly, the descent of the body whorl. The second of the two ratios expresses the relationship between the increase in diameter of the body whorl with increasing shell length. A similar result might easily be obtained by using the ratio shell length/shell diameter but with the technique of measurement employed the width of the aperture was more accurately obtainable than the maximum diameter of the shell. Text-figs. 2 and 3 show these two ratios plotted against shell length ; in both it can be seen that there is an increase in the value of the ratio with increasing shell length. The change in the values is so slight that the means of the ratios provide a good index of shell form. The graph l/ml plotted against shell length

(Text-fig. 3) shows an interesting feature. For small shell lengths the graph is practically a straight line parallel to the horizontal axis and the upward slope only becomes apparent after the 6·5 mm. shell length mark. As pointed out earlier, this is the approximate shell length at which adult anatomical characters become developed and the change in form of the shell at this point is, presumably, a reflexion of the anatomical changes. The actual change in form which the shell exhibits may be explained thus : in its early stages the spire is completely depressed, subsequent whorls being added around the preceding ones ; at the onset of maturity the accessory genital glands increase in size very rapidly necessitating an increase in shell volume to accommodate them and this is achieved by the body-whorl moving downward in relation to its predecessor, giving an increase in shell length without a corresponding increase in aperture length.

The means and standard deviations of these two ratios in the population under consideration are

l/ml	mean 1·17	s.d.	± 0·08
l/mb	mean 2.31	s.d.	± 0·143

THE MANTLE

The mantle markings of *B. jousseaumei* from the Gambia consist of patterns of small black spots and patches scattered irregularly over a light grey field. The spots often appear dark grey rather than black owing to the pigment granules of which they are composed being only loose aggregations rather than dense concentrations.

The nephridial ridge on the underside of the mantle may be well developed or almost absent. It is often present only on the distal end of the kidney. The intermediate ridge is almost always well developed and is about equal in length to the kidney. An examination of transverse sections of the mantle has failed to show the presence of ciliated epithelium on this intermediate ridge (described for *B. africana* by Hubendick, 1948) but this may be due to the method of fixation employed.

THE RADULA

The radula is in no way remarkable. The number of tricuspid laterals varies from six to eight in each transverse half-row. This number does not appear to change with the age of the snail, but the number of marginal teeth does appear to increase in older specimens. It is perhaps worthwhile recording here that the first lateral tooth is tricuspid (Text-fig. 4). Dupuis and Putzeys (1923) mention as the only real difference between *Physopsis* and *Isidora* that the first lateral in the former group is bicuspid while in the latter it is tricuspid. The endocone of the first lateral is often difficult to observe and it is doubtless this fact that gave rise to the erroneous statement of these authors.

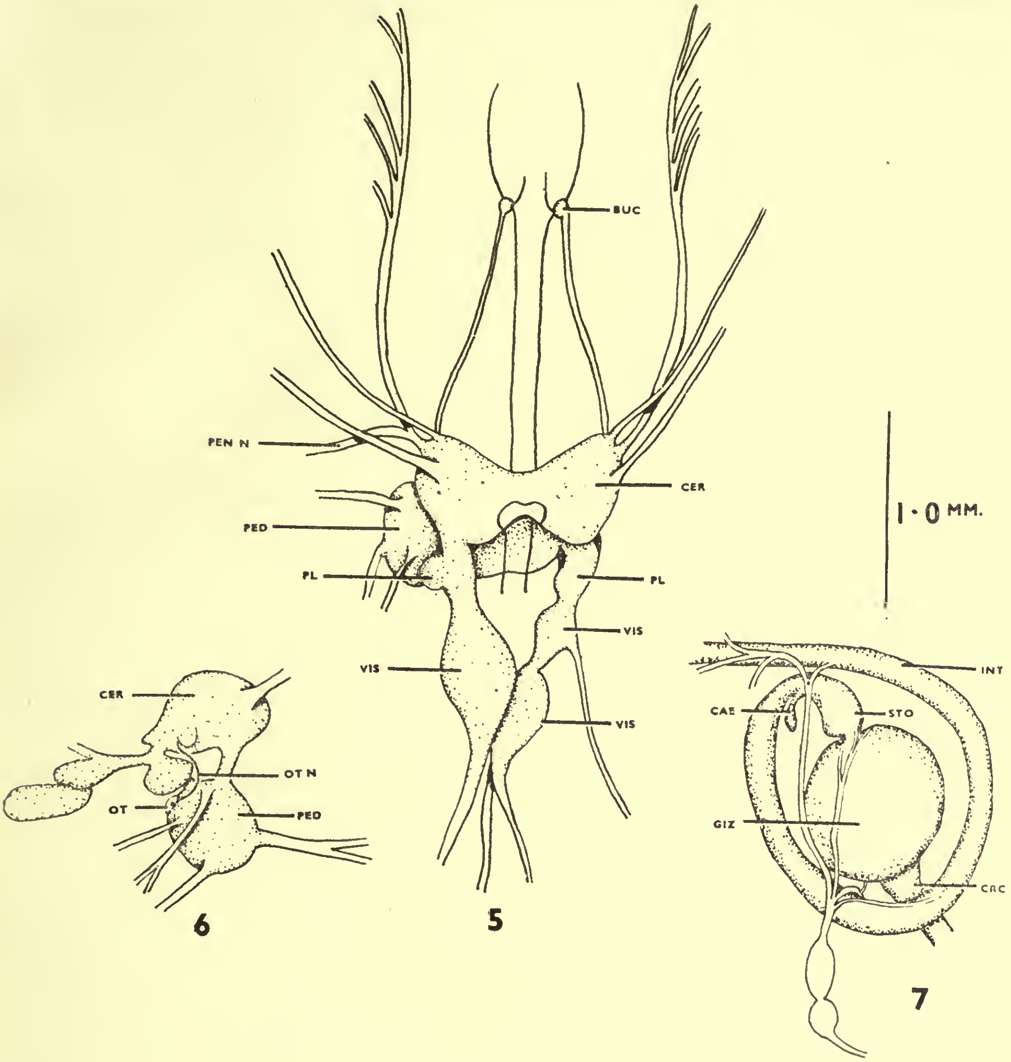
CENTRAL NERVOUS SYSTEM

The central nervous system in the Planorbidae shows little variation between the various genera. The connectives between the ganglia are relatively long in *B. jousseaumei*, but since the material on which these anatomical observations are based was all narcotized and well extended such details may not be strictly comparable with those of other workers (Text-fig. 5).

The penial nerve appears to be a composite structure with its main source in the left cerebral ganglion ; a number of other fibres running with the main component arise from the left pedal ganglion. The cerebral part of the nerve branches off from a larger trunk arising near the origin of the left cerebro-buccal connective and passing forwards giving off finer branches to the sides of the head and lips. It is probable that the nerves arising from the cerebral ganglia have a primarily sensory function, while those from the pedal ganglia are mainly motor. This would mean that the composite nature of the penial nerve provides both sensory and motor innervation for the copulatory organ. The principal nerve arising from the dorsal surface of each of the cerebral ganglia runs to the tentacle, its associated lobe and the eye on the same side of the body as that from which it arises. The pedal ganglia send several large nerves down into the foot and running back from the two buccal ganglia is a pair of fine nerves, one on either side of the oesophagus. The three visceral ganglia send nerves to the organs in the visceral mass and one large trunk arising from the left visceral ganglion passes to the anal lobe and pseudo-branch, while a similar large trunk from the right visceral ganglion passes upwards to the mantle. Contributory evidence as to the sensory nature of the cerebral ganglia is obtained from the otocyst which, although partially embedded in the posterior side of the pedal ganglion appears to be innervated solely from the cerebral ganglion above (Text-fig. 6).

BLOOD CIRCULATORY SYSTEM

The heart lies within its extremely delicate pericardium on the mantle close to the proximal end of the kidney, above the point at which the oesophagus passes into the crop. The auricle receives blood from the very large vein running along the anterior edge of the kidney. The aorta leaving the ventricle is variable in length, it may pass right over the intestinal loop which curves round the gizzard before dividing (Text-fig. 7) or it may divide so far back that the ventricle has a bifid appearance. In either case, the lesser of the two branches follows the intestine on its course round the gizzard while the major branch passes upward over the posterior edge of the gizzard. As it passes over the space between the intestine and gizzard a very large artery passes down between these two organs and divides almost at once, one branch going to the crop and distal side of the gizzard, the other to the accessory genital glands and the head cavity. A short distance after this division of the main branch from the aorta a smaller branch is given off to supply the stomach and proximal part of the gizzard and the rest of the vessel continues up the side of the gizzard, past the point at which the digestive gland opens from the intestine, and then, giving off a number of side branches into the digestive gland, follows the path of the intestine as it loops up into the upper whorls of the body. The principal artery to the head follows beneath the oesophagus to the circum-oesophageal nerve ring where vessels supplying the ganglia are given off ; then, after passing through the nerve ring it divides. One branch passes vertically downwards as the pedal artery and the other continues forward to the underside of the buccal mass where the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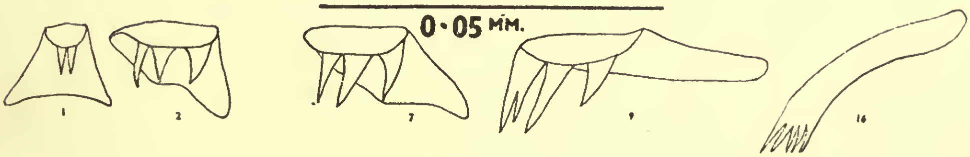
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FIG. 4. Radula teeth of *B. jousseaumei* from Gambia.

FIG. 5. Central nervous system of *B. jousseaumei*.

Fig. 6. Right lateral view of central nervous system of *B. jousseaumei* to show the otocyst and its innervation

FIG. 7. Heart and principal arteries of *B. jousseaumei*.

(Figs. 5, 6 & 7 to same scale.)

vessel dilates before breaking up into fine branches supplying the muscles of the mass and the sides of the head and lips. A fine lateral branch which leaves the main trunk in the region of the nerve ring serves the penial complex. It runs parallel with the penial nerve and appears to enter the complex at the junction of the penis sheath and preputium.

ALIMENTARY SYSTEM

The digestive tract in the Planorbidae is so well known and subject to so little variation that it is not necessary to enter into a full description here.

REPRODUCTIVE SYSTEM

The gross morphology of the genital tract of *B. jousseaumei* has already been described (Wright, 1956). It is intended here to consider the histology of the tract and its development. Hubendick (1948 *a* & *b*) has described the anatomy and histology of the male copulatory organs of several species of *Bulinus*. Larambergue (1939) has described fully the reproductive anatomy and histology of *Bulinus truncatus*. Abdel-Malek (1954 *a* & *b*) has given detailed accounts of the morphology and histology of the genital organs of two Planorbids *Helisoma trivolvis* (Say) and *Biomphalaria boissyi* and comparisons between all of these and *Bulinus jousseaumei* will be made.

Histologically no real differences were found between Abdel-Malek's description of the ovotestis in *Biomphalaria* and *Helisoma* and that in the present species. The acini are enveloped in " Ancel's layer " of thin connective tissue and the germinal epithelium within this layer appears to line only the lower parts of the acini. Heavily pigmented connective tissue is largely confined to the layer covering the top of the organ. In the adult snail all stages of spermatogenesis and oogenesis can be observed in the same acinus. Young oöcytes and spermatids are largely confined to the lower parts of the acini and the upper parts are occupied by maturing ova, as many as six having been seen in a single acinus as compared with two to three reported by Abdel-Malek in *Helisoma trivolvis*. The mature ova are enclosed within a follicular membrane made up of nurse cells and connective tissue. Mature spermatozoa are more or less ubiquitous in the acini, either free in the lumen or attached by their anterior ends to basal " Sertoli " cells. The motility of these basal cells is shown in that they may be found on the outer wall of the follicles of maturing ova, a position that could only be reached by their independent locomotion. The hermaphrodite duct is lined with an epithelium of cuboidal cells bearing short cilia and the duct is sheathed in a thin layer of connective tissue (Text-fig. 8). The epithelium lining the seminal vesicles is similar to that in the hermaphrodite duct but the median

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FIG. 8. Transverse section of hermaphrodite duct of *B. jousseaumei*.

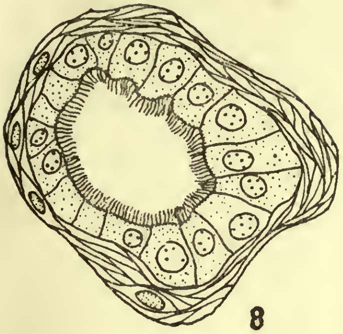
FIG. 9. Transverse section of first part of sperm duct of *B. jousseaumei*

FIG. 10. Transverse section of sperm duct of *B. jousseaumei*.

FIG. 11. Epithelial lining of prostate tubule of *B. jousseaumei*.

FIG. 12. Transverse section of vas deferens within body wall of *B. jousseaumei*.

FIG. 13. Transverse section of vas deferens in head cavity of *B. jousseaumei*.



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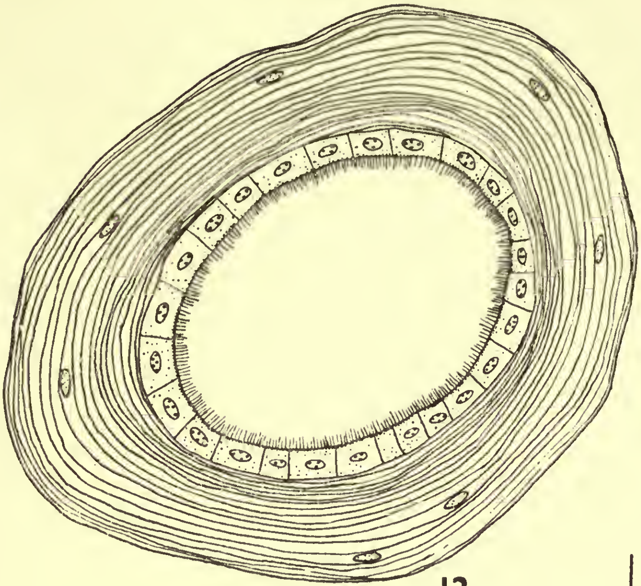

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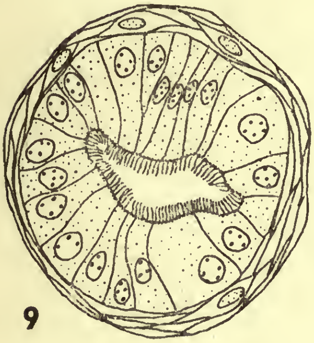

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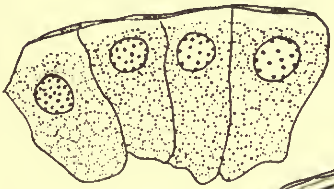

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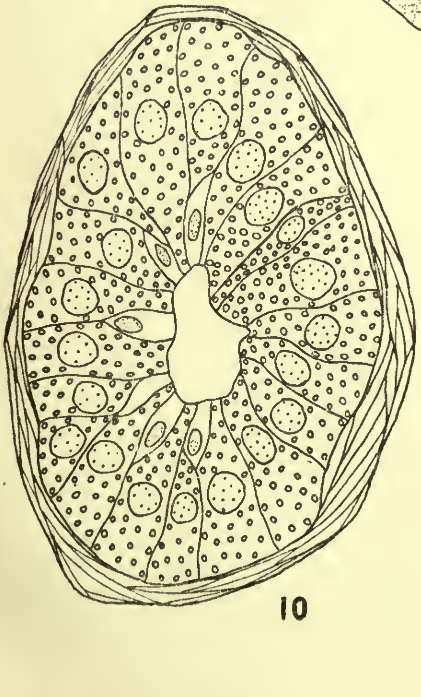

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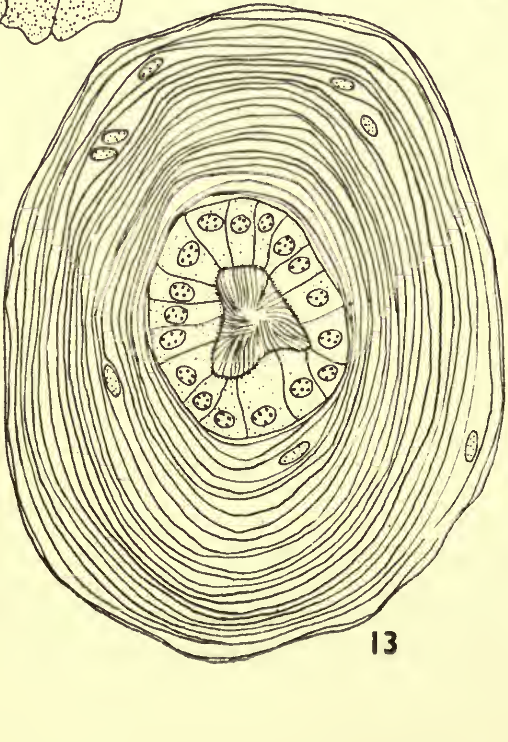

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nuclei are a little larger and the cytoplasm is more granular. The separation of the male and female ducts from the common duct occurs at a point well embedded in the base of the albumen gland. The sperm duct at its source is narrow with a small lumen lined by short columnar epithelial cells, ciliated, and with median to basal nuclei and finely granular cytoplasm (Text-fig. 9). This part of the duct is quite short and it soon becomes considerably larger in diameter although the size of the lumen does not increase greatly. The epithelium lining the duct loses its cilia and the cells are of a much taller columnar type with median nuclei, larger than those in the earlier part of the duct, and the cytoplasm is filled with large, eosinophilic, refractile granules. A few wedge-shaped cells occur between the apical ends of the columnar type and these do not contain the eosinophilic refractile granules (Text-fig. 10). The sperm duct retains this histological structure right up to its entry into the prostate gland. Hubendick (1948*a*) in discussing the structure of the prostate in *Bulinus* has shown that in *B. inflatus*, an Australian species, the tubules of the prostate open individually into the vas deferens which enters the gland at the proximal end and leaves it distally, a structure similar to that in *Physa*. In *B. jousseaumei* however the prostate is a discoidal structure, flattened on one side and convex on the other. The sperm duct enters the gland almost in the centre of the flattened surface and the vas deferens leaves it also almost in the centre. There is therefore a central point at which the tubules of the prostate discharge their secretion into the male duct and it is at this point that the histological structure of the male duct changes from the typical form of the sperm duct to that of the vas deferens. The tubules of the prostate gland are close-packed, each is ensheathed in a thin-layer of connective tissue and is lined by large secretory cells with large basal nuclei with granular contents. The cytoplasm of these cells is eosinophilic and not granular (Text-fig. 11). There are some basophilic cells near the blind ends of the tubules. As the vas deferens leaves the prostate it is lined with sparsely ciliated epithelium of rather flattened cuboidal cells with central nuclei containing sparse chromatin granules. This epithelium is surrounded by a thin layer of circular muscle. As the duct proceeds on its course there is an increase both in the ciliation of the lining epithelium and in the thickness of the circular muscle layer. Where the duct passes through the body wall the lumen is large, the cells of the epithelial lining are wider than high, the cilia are plentiful but not long and the muscle layer is thick (Text-fig. 12). After leaving the body wall and entering the head cavity the structure of the vas deferens changes slightly. The lumen becomes more restricted, the epithelial lining more columnar, with basal nuclei, still with few chromatin granules in the clear nucleoplasm, the cilia become longer and the muscle layer thicker (Text-fig. 13). At the point of entry into the penis sheath the duct becomes the epiphallus which lies coiled in the upper part of the sheath and which has a very different appearance in section (Text-fig. 14). The overall diameter is reduced but that of the lumen remains more or less unchanged. The internal epithelium is of irregularly cuboidal cells with central nuclei and no cilia. The nuclei are densely packed with chromatin and stain deeply in haematoxylin. The epithelial layer is surrounded by a layer of circular muscle and outside this is a layer of transverse muscle and connective tissue with bundles of longitudinal muscle fibres embedded in it. The transition from epiphallus to penis proper is gradual. Due to the mode of operation of the copulatory organ in *Bulinus* [Larambergue (1939) and Hubendick (1948*b*)] the part that is proximal when the organ is at rest is distal when it is erected and the distal resting part is proximal during copulation. The following description is based on resting specimens. Proximally, the lumen increases gradually, the epithelial lining becomes regularly cuboidal and the central nuclei are less deeply staining. At about the maximum diameter of the penis the lumen is partially occluded by profound folding of the lining. The epithelium is of cuboidal cells with central nuclei containing sparse chromatin granules and beneath this is a layer of connective tissue with transverse muscle fibres and blood spaces. Around this is a layer of muscle and the outer layer is of mixed muscle fibres with blood spaces and connective tissue (Text-fig. 15). The distal tip of the penis, just before the point where it unites with the penis sheath, has a tri-radiate lumen surrounded by the same sort of epithelium as before and outside this only a thin layer of circular muscle (Text-fig. 16). The penis sheath has an outer covering of a thin, flattened epithelium within which is a layer of mixed muscle fibres followed by an innermost layer of almost pure circular muscle. The lining of the preputium is thrown into a number of folds with two muscular pillars predominating. Usually only one of these two pillars extends the whole length of the preputium, the other usually fades out before the junction with the penis sheath at the upper end. The position of the pillars within the preputium coincides with the point of attachment on the outside of two series of muscle fibres that connect the organ to the body wall of the head cavity. The epithelial lining of the preputium is fundamentally of columnar or cubical cells with more or less basal nuclei. In the most proximal parts of the organ a few ciliated cells are present. Distributed irregularly are gland cells, much larger than the other components of the epithelium, with basal nuclei often displaced to one side of the cell (Text-fig. 17). The cytoplasm of these gland cells may be either coarsely granular and eosinophilic or much more finely granular and staining deeply in haematoxylin. They are often clustered together in patches and may penetrate quite deeply into the muscular layers beneath. They are more common in the upper proximal parts of the organ but in one specimen examined they were confined almost exclusively to the epithelium covering one of the muscular pillars. Beneath the epithelium is a layer of circular muscle and outside this a thick layer of mixed muscles and connective tissue with blood spaces.

Returning to the point of separation of the hermaphrodite duct, the female tract begins with a short duct with a narrow lumen lined by columnar glandular cells with darkly-staining basal nuclei. Between the free ends of these columnar cells are wedge cells with nuclei containing few chromatin granules. These wedge cells bear short cilia (Text-fig. 18). This short duct opens into the carrefour which has a wide lumen and a folded wall. The epithelial lining (Text-fig. 19) is of tall columnar cells and wedge cells. The glandular columnar forms have dark staining basal nuclei. There are patches of ciliated cells particularly in the folds of the wall. Opening into the carrefour is the duct from the albumen gland. This gland is made up of numbers of tubules with loose connective tissue between them. The lining of the tubules is quite characteristic in section ; it consists of roughly cuboidal cells with basal granular nuclei and with numbers of large droplets in the cytoplasm. These droplets stain deeply in haematoxylin (Text-fig. 20). Distally to the carrefour the oviduct is lined with a columnar epithelium containing a few wedge cells and a few gland cells but without cilia (Text-fig. 21). The oviduct leads into the uterus which is elongate transversely in cross section. The epithelial lining is similar to that of the oviduct but there are more gland cells, some with acidophilic and some with basophilic granules in the cytoplasm. There are also a few ciliated cells (Text-fig. 22). For a considerable part of its course the uterus is surrounded by the muciparous gland. Macroscopically this gland is smooth, colourless and rather translucent in appearance. In section it is seen to be made up of close-packed tubules with little intervening connective tissue. The tubules are lined with large, irregularly cubical cells with darkly staining basal nuclei. The cytoplasm is entirely without granules and is completely unstained by either haematoxylin or eosin (Text-figs. 23). The tubules open individually into the dorsal side of the uterus. Following immediately after the muciparous gland the uterus passes into the oöthecal gland, distinguished macroscopically by its opaque white appearance in contrast to the translucent colourlessness of the previous gland. Internally the uterine wall is deeply folded in this region. The epithelium (Text-fig. 24) consists almost entirely of tall columnar glandular cells with basal nuclei. Both acidophils and basophils are present but the coarsely granular or eosinophilic type of cytoplasm predominates. A few patches of ciliated cells are present and the glandular cells may be several layers thick in places, penetrating deeply into the underlying connective tissue. The transition from the folded, glandular wall of the oöthecal gland to the tubular, ciliated vagina is quite abrupt. The epithelial cells in this part are of a short columnar type with median to basal nuclei containing sparse chromatin granules. The cytoplasm of these ciliated cells is very finely granular and eosinophilic (Text-fig. 25). The seminal receptacle duct which opens from the vagina is lined in its distal part (that nearest to the vagina) with a columnar epithelium with basal nuclei and finely granular acidophilic cytoplasm but without cilia. The rest of the duct lining is similar but the columnar cells are taller and ciliated. The distended sac of the

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FIG. 14. Transverse section of epiphallus of *B. jousseaumei.*

FIG. 15. Part of transverse section of penis of *B. jousseaumei.*

FIG. 16. Transverse section of tip of penis of *B. jousseaumei.*

FIG. 17. Part of epithelial lining of the preputium of *B. jousseaumei* showing basophilic and eosinophilic gland cells.

FIG. 18. Epithelial lining of proximal part of oviduct of *B. jousseaumei.*

FIG. 19. Epithelial lining of carrefour of *B. jousseaumei.*

Fig. 20. Epithelial lining of albumen gland tubule of *B. jousseaumei.*

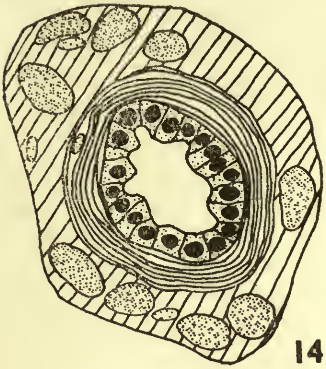
FIG. 21. Epithelial lining of distal part of oviduct of *B. jousseaumei.*

FIG. 22. Epithelial lining of uterus of *B. jousseaumei.*

FIG. 23. Epithelial lining of muciparous gland tubule of *B. jousseaumei.*

FIG. 24. Epithelial lining of oöthecal gland of *B. jousseaumei.*

FIG. 25. Epithelial lining of vagina of *B. jousseaumei.*



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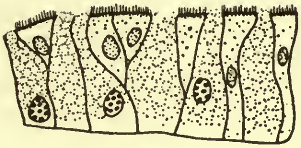

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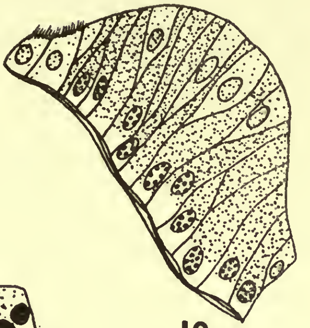

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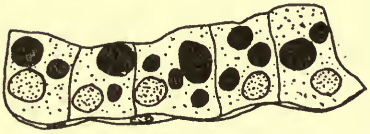

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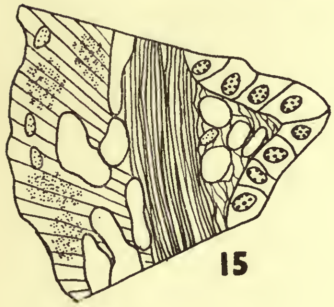

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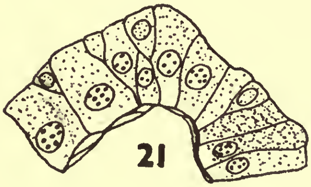

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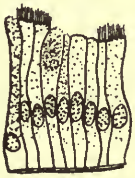

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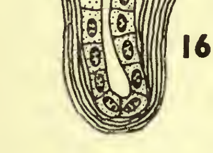

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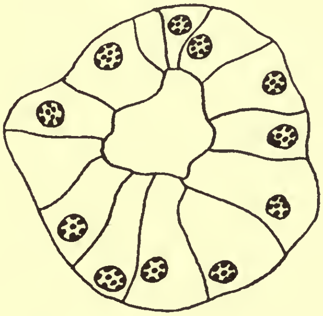

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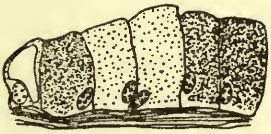

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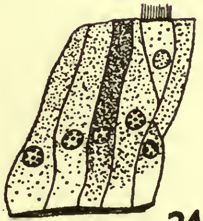

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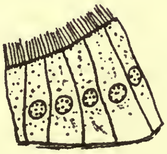

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receptaculum is thin walled, a thin layer of connective tissue lying outside a tall columnar epithelium with basal nuclei and indistinct cell boundaries.

The foregoing description is based on a study of sections of the genital organs of several adult snails in the 8·0–9·5 mm. shell length range. For comparison series of sections were cut through the reproductive organs of a juvenile snail (4·5 mm. shell length) and an " adolescent " specimen 5·7 mm. long.

The gonad of the juvenile showed neither mature ova nor spermatozoa. Active cell division appeared to be in progress in the zone of the germinal epithelium near the bases of the acini but the state of fixation of the specimen made definite observations difficult. No sections of the haemaphrodite duct were obtained. The male tract was not clearly defined until the level of the prostate gland. This organ was present but in section the tubules although defined were lined with an undifferentiated cuboidal epithelium with central nuclei. The vas deferens leading from the prostate was lined with a similar unciliated epithelium. The sheath of circular muscle present in the adult snail was represented by close-packed undifferentiated connective tissue cells. The duct remained more or less unchanged in this condition throughout its course. The epiphallus was again ensheathed in undifferentiated tissue and the epithelial lining was of more columnar cells with basal nuclei. The penis and penis sheath at this stage also showed no clear definition of muscle tissue and the separation between the muscle layers of the two parts was just becoming apparent. The folding of the inner wall of the penis was already in evidence. The preputium also was surrounded by undifferentiated muscular tissue and the lumen, already S-shaped owing to the development of the two main muscular pillars, was lined with a cuboidal epithelium with central nuclei. Of the female system at this stage little can be said. The uterus and vagina are present as tubes lined by a uniform epithelium. The albumen gland is entirely undeveloped, likewise the muciparous and oöthecal glands. The receptaculum seminis and its duct are present but the receptacle sac is scarcely more than a slight dilatation of the duct. The only evidence of differentiation in the female tract in this specimen is that the nuclei of the epithelial cells in the regions that will become glandular stain more deeply in haematoxylin than do those of the other regions.

The gonad of the " adolescent " snail (5·7 mm. shell length) showed clusters of mature spermatozoa in the acini with a few maturing oöcytes in the upper parts. Some of the largest of these oöcytes showed dividing nuclei and were, presumably, undergoing maturation division. Sections of the seminal vesicle and hermaphrodite duct were packed solidly with spermatozoa. The sperm duct after its separation from the common duct shows the same short, ciliated part followed by the long, glandular part with refractile eosinophil granules in the cytoplasm as is found in the adult. The prostate gland also is identical histologically to the adult. Throughout its course the vas deferens corresponds in histological detail to the form already described in the adult. The transition to the epiphallus is similar as are the structures of the penisand penis sheath. The preputium, however, is, in its distal part, similar to that in the juvenile in that the lumen is S-shaped and only two muscular pillars are present. More proximally additional folds in the wall do occur. The epithelium lining the lumen is more ciliated than in the adult and few gland cells have been observed. The female tract at this stage is far less well developed. The albumen gland is represented by a fairly compact mass of tissue of undoubtedly glandular nature but scarcely organized into tubules as in the adult. The few tubules which are present are not lined with the characteristic glandular epithelium of the adult but with cells which probably later develop into this form. The carrefour is present as a dilatation of the oviduct but its epithelial lining is only differentiated into glandular areas in parts, some cilia are also present. The oviduct is similar histologically to that in the adult and it in turn passes into the ciliated part of the uterus. Neither the muciparous nor the oöthecal glands is represented by more than a slight thickening of the uterine wall. The receptaculum seminis is well developed and contains spermatozoa and the vagina is strongly ciliated.

These histological observations support the opinion already formed from gross anatomical studies that the male genital tract develops slightly earlier than the female system. Morton (1954) has suggested that a protandrous sexual cycle is the primitive condition in gastropods and that simultaneous hermaphroditism has been later developed in the higher pulmonates and opisthobranchs. Larambergue (1939) states that in *Bulinus contortus* there is no protandry since spermatozoa and ova are produced simultaneously throughout life even though spermatozoa do appear first. It seems probable that the earlier development of the male tract is a relic of the primitive protandrous condition which has become almost completely obscured, particularly where the length of the breeding season is limited by adverse environmental conditions.

To complete this histological study of the genital organs of *B. jousseaumei* a few comparisons with similar studies on related forms should be considered. It has already been said that there are no differences between the fundamental structure of the gonad in this species and in *Biomphalaria boissyi* and *Helisoma trivolvis* as described by Abdel-Malek (loc. cit.) and it is probable that this structure is fairly uniform throughout the Planorbidae. The hermaphrodite duct corresponds to the description by Larambergue (loc. cit.) for that in *B. contortus*, also the point of separation of the male and female tracts. The sperm duct differs from that in *B. contortus* in that no ciliation has been observed in its lumen apart from the very short part immediately after its separation from the common duct. Abdel-Malek mentions no ciliation of the sperm duct in *B. boissyi* and only near the prostate in *H. trivolois*. In both of these species he mentions the refractile, eosinophilic, cytoplasmic granules but also records the presence of scattered basophils not seen in *B. jousseaumei*. The prostate corresponds well with that described by Larambergue for *B. contortus* and this author stresses the fact that the gland is not traversed by the male duct but that its tubules open into a central chamber into which the sperm duct opens at one side and from which the vas deferens leaves at the other. The vas deferens in *B. jousseaumei* differs from that in *B. contortus* in that it is ciliated throughout its length while Larambergue reports that in the second species the epithelium is unciliated and of a mucous-secreting type. In both of the species described by Abdel-Malek the vas deferens is ciliated throughout its length although, due to the different form of the prostate in these species, there is only a gradual transition from the form of the sperm duct to that of the vas deferens instead of a clear-cut demarcation of the two as in *B. jousseaumei*. The epiphallus which is so well differentiated from the vas deferens in the present species was also noted (although not under this name) by Larambergue to be histologically different. Since the structure of the copulatory apparatus in the species described by Abdel-Malek differs so markedly from that in the Bulinids it is not possible to draw comparisons between the histology of the two but it is interesting to note that in his species the seminal canal within the penis (and therefore that part of the male duct actually inside the penis sheath) is ciliated and that the epithelial lining does not differ from that of the vas deferens. The histological structure of the penis, penis sheath and preputium in the present species show no significant differences from those described by Hubendick (1948*b*) and Larambergue. Larambergue does not describe the histology of the female genital tract of *B. truncatus* apart from mentioning the ciliation of the receptaculum seminis duct. The epithelial linings of the first part of the oviduct and of the carrefour are similar to those of *B. boissyi* and *H. trivolvis* although not so heavily ciliated. Beyond the carrefour the epithelium of the oviduct in the present species almost entirely lacks cilia while these are present in *Biomphalaria*. The epithelium of the uterus is similar in the two species, and the muciparous gland merges gradually with the uterus rather than abruptly as in *Helisoma*. The remainder of the female tract is very similar to *Biomphalaria* except that the part of the receptaculum seminis duct nearest to the vagina is unciliated, a condition similar to that in *Helisoma*.

RELATIONSHIPS OF *B. JOUSSEAUMEI*

In considering the affinities of *B. jousseaumei* it is necessary to review the species of the sub-genus *Physopsis* known from West Africa. For this purpose it is often necessary to refer to the medical literature as it is largely in works on the epidemiology and transmission of human schistosomiasis that records of intermediate hosts are to be found. The only species of *Physopsis* actually described from West Africa is *P. globosa* (Morelet, 1866) collected in Angola. Of the other twenty or so species, all were described originally from East or South Africa. The question of the identity of *P. globosa* with *P. africana* Krauss, 1848, will not be dealt with here since opinions are still divided on this point and much detailed work must be carried out before a solution of the problem can be reached. It must, however, be pointed out that many authors now treat *P. globosa* as an absolute synonym of *P. africana* others consider it to be a variety or sub-species of the latter while still others recognize it as a separate species. In the following account it will be pointed out (where it is known) which of these three courses was adopted by the workers concerned. Since a chronological account of these records would undoubtedly prove confusing, they are presented in a geographical sequence from north to south.

McCullough & Duke (1954) were the first to record *Bulinus africanus* from the Gambia and they noted that this was probably the northernmost record for the species in West Africa. They were following the classification of Amberson & Schwarz (1953) who treated all species of *Physopsis* as forms of *B. africanus* and there is no doubt that their record refers to *B. jousseaumei*. I later recorded (Wright,

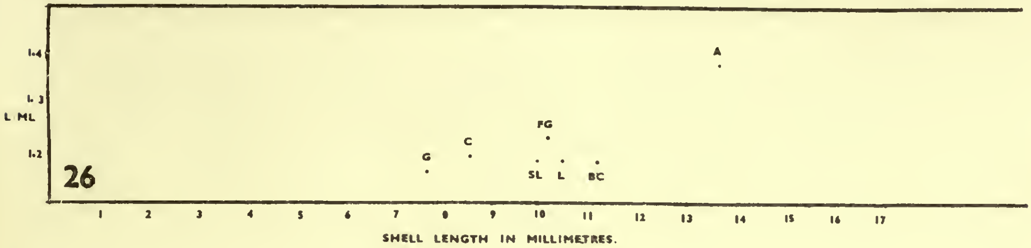
1956) a form of *B.* (*P.*) *globosus* from one localty in Upper River Division, Gambia, as well as *B. jousseaumei* from the Casamance Province of Senegal, the next territory to the south of the Gambia. No published records of *Physopsis* from Portuguese Guinea have been found, and Pinto (1949) in a recent survey of vesicle schistosomiasis in that territory found only *Bulinus forskali* and *B. dautzenbergi.* Vogel (1932) in a similar survey in French Guinea and Liberia found (and illustrated) *Physopsis globosa.* More recently in a rather confusing account of schistosomiasis in French West Africa, Le Gall (1944) mentions as a probable vector of urinary schistosomiasis in French Guinea "*Physopsis ovoides* and *boissyi*" from Kissidougon. This presumably refers to *P. ovoideus* and *Biomphalaria boissyi.* The next territory southwards from the French Guinea coast, Sierra Leone, is perhaps one of the best documented areas in tropical Africa with respect to the epidemiology of schistosomiasis. It has been the subject of three major surveys. Blacklock (1924), Blacklock & Thompson (1924), Blacklock (1925), Gordon, Davey & Peaston (1934) and Gerber (1952). Connolly (1928) published an account of the freshwater molluscan material collected by Blacklock and considered the *Physopsis* to be *P. globosa* with strong affinities to *P. didieri.* He mentioned the presence of a well-marked spiral sculpture on the material from Sierra Leone, a feature which he had not observed on *P. globosa* from Angola and Mozambique. Connolly also identified material submitted to him by Gordon and his co-workers and identified the *Physopsis* as *P. globosa.* Gerber submitted his material to Dr. W. J. Rees who identified one fully-grown and three smaller specimens out of a batch of 204 shells as *Bulinus globosus* and referred the remaining 200 to *B. africanus.* The same sample of shells was shown to Berry who pronounced them all to be *Physopsis africana.* To the south of Sierra Leone is Liberia and here Vogel (loc. cit.) records *Physopsis globosa* and Veatch (1946) mentions *Physopsis africana* var. *globosa* as the intermediate host of *Schistosoma haematobium* in the Western Province. No records of identified *Physopsis* from the Ivory Coast have been seen but Ingram (1924) incriminated *P. globosa* as the possible vector of urinary schistosomiasis in the Gold Coast ; more recently Edwards & McCullough (1954) have demonstrated that the parasite is carried by *P. africana* but they also mention that they consider *P. globosa* to be either a race or an absolute synonym of this species. The only further record of an identified *Physopsis* between the Gold Coast and the Belgian Congo is that of *P. globosa* collected at Kano in Northern Nigeria (Gordon, 1932). In the excellent work of Pilsbry & Bequaert (1927) a variety of *P. africana* is recorded from a number of localities in the Belgian Congo, also *P. africana globosa.* These authors refer the other recorded species of *Physopsis* (apart from *P. tanganyicae* von Martens) from the Belgian Congo either to *P. africana* var. or to *P. africana globosa.* Finally, the territory to the south of the Belgian Congo, Angola, is the type locality for *P. globosa* Morelet.

Examination of material from French Guinea, Sierra Leone, Liberia, Belgian Congo and Angola has shown that without doubt the same species of *Physopsis* is present in all these territories and that *B. jousseaumei* is a form of that species. The table below gives the mean dimensions in millimetres of the populations examined from the territories mentioned above ;

Territory and number of specimens	Shell length	Shell max. diam.	Aperture length	Aperture width	Shell length / Aperture width	Shell length / Aperture length
Gambia	7·84	6·00	6·65	3·37	2·31	1·17
283	±1·52	±1·12	±1·03	±0·66	±0·14	±0·08
Casamance	8·69	6·32	7·21	3·60	2·41	1·20
20	±0·96	±0·76	±0·70	±0·33	±0·13	±0·04
French Guinea	10·33	7·01	8·31	4·04	2·55	1·24
20	±0·75	±0·42	±0·51	±0·20	±0·11	±0·05
Sierra Leone	10·07	7·18	8·43	3·97	2·55	1·19
100	±2·06	±1·75	±1·43	±0·93	±0·19	±0·08
Liberia	10·56	7·38	8·8	4·28	2·47	1·19
6	±2·81	±1·63	±1·98	±1·06	±0·15	±0·07
Belgian Congo	11·34	8·50	9·51	4·54	2·48	1·19
100	±1·64	±1·22	±1·52	±0·63	±0·11	±0·065
Angola (Type series)	13·43	9·51	9·60	5·13	2·62	1·40
26	±2·19	±1·63	±1·48	±0·85	±0·15	±0·085

Text-fig. 26 shows the means for the ratio Shell length/Aperture length plotted against the mean lengths for each of these samples. Text-figs. 27–30 show the ratios shell length/aperture length and the frequency distributions of shell length in the samples from Sierra Leone and the Belgian Congo.

Reference to the table shows a gradual decrease in the dimensions of the shell from south to north. The composition of the samples is not wholly comparable, those from the Gambia, Sierra Leone and Belgian Congo are more or less random population samples with a proportion of juveniles and those from Casamance, French Guinea and the type series from Angola contain mostly adult specimens. The small sample from Liberia consisted of four adults and two juveniles, hence the rather large standard deviations. The means of the type series differ from those given by Mozeley (1939) because his figures were based on ten specimens of the series only. In addition to the discrepancies in sampling certain differences due to ecological conditions also occur. The most obvious of these is the " still water " effect. Schwetz (1954) has described the effect of changed environment on shell form in several planorbid snails and the exsertion of the spire in forms which develop in static water compared to those in gently moving streams is well known. This accounts largely for the difference in the mean values of the ratio shell length/aperture length in the type series and in the Belgian Congo sample. The latter came from a pool in a recently dried stream bed while Morelet (1868) notes that the Angolan material was collected in a lake. Similarly this probably accounts for some of the differences between Gerber's and Blacklock's specimens from Sierra Leone. Gerber's material from the still waters of a rice swamp has a more exserted spire than Blacklock's from a stream.



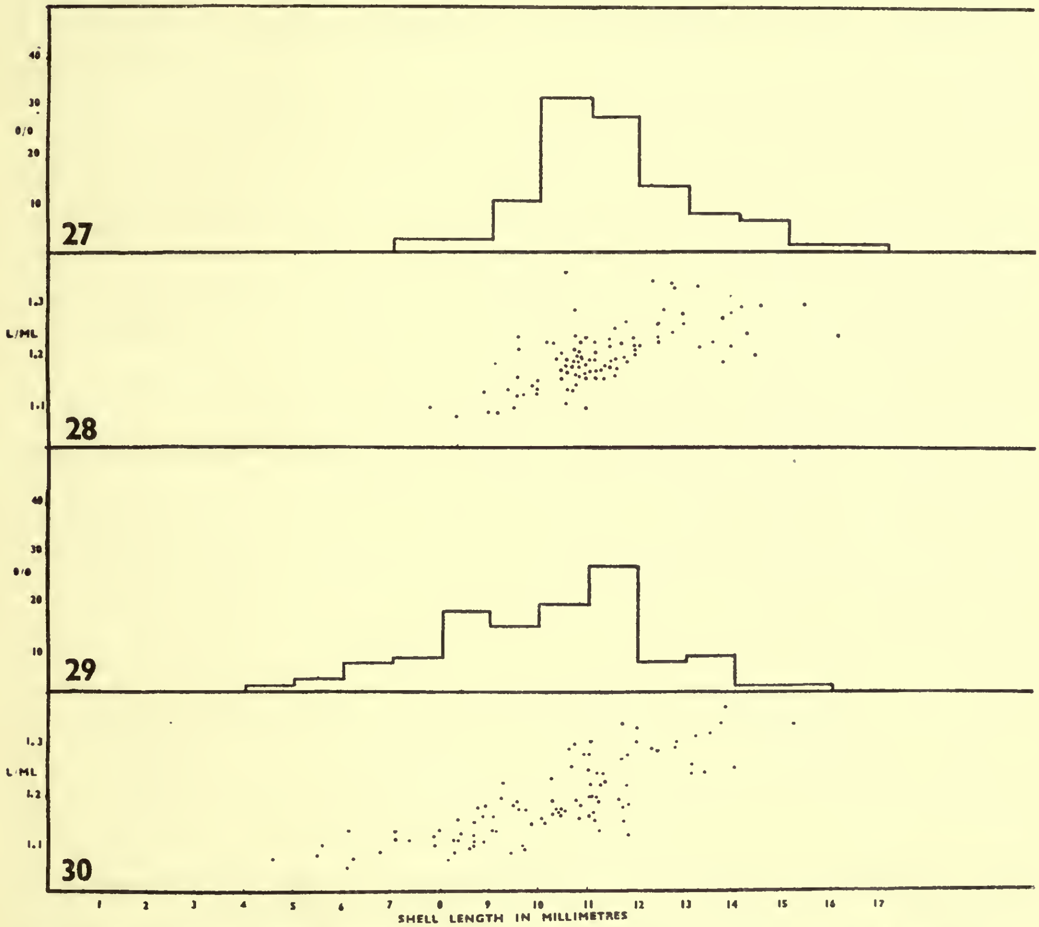


FIG. 26. Graph of mean ratio shell length/aperture length against mean shell length for populations of *B. jousseaumei* from Gambia (G), and Casamance (C) and *B. globosus* from French Guinea (FG), Sierra Leone (SL), Liberia (L), Belgian Congo (BC) and the type series from Angola (A).

FIG. 27. Size-frequency histogram for a population of *B. globosus* from Belgian Congo.

FIG. 28. Graph of ratio shell length/aperture length against shell length for the same population.

FIG. 29. Size-frequency histogram for sample of *B. globosus* from Sierra Leone.

FIG. 30. Graph of ratio shell length/aperture length against shell length for the same population.

The general form of the shell is similar throughout the whole range under consideration (Plate I). In the same population shells may be seen with the columella margin fused entirely to the body whorl and others with a space between the two. This was stressed by Connolly (1934) as being the only constant conchological difference between *Physopsis africana* and *P. globosa.* There is also a range of variation in the angle at which the outer lip meets the body whorl at the top of the aperture, a character used by Pilsbry & Bequaert (1927) for the separation of the same two species. The sculpture pattern described earlier for the Gambian material is found also throughout the range, being most marked in the specimens from Sierra Leone (Plate 2,) and, as noted by Connolly (1928) practically absent from the Angolan material. This is of interest since Mandahl-Barth (1954) erected a sub-species *Bulinus globosus ugandae* which he separated from the nominate sub-species because it completely lacked the spiral sculpture of the typical form. In passing it seems appropriate to note that amongst the shells collected in Northern Rhodesia by Buckley (1946) were a number of specimens labelled by Connolly as juvenile *Bulinus natalensis* but which were also referrable to *B. hemprichii depressus* Haas, 1936. These specimens were indistinguishable from many of the juvenile *Physopsis globosa* seen during this work. Unfortunately the type specimens of Haas' subspecies were destroyed or lost during the war but from a study of the photographs of these specimens there can be little doubt that the sub-species should be placed in the synonymy of *Bulinus* (*Physopsis*) *globosus*.

It can be seen from Text-fig. 30 that the pattern of the graph of shell length/aperture length against shell length for the sample from Sierra Leone is similar to that for the Gambian population (Text-fig. 3). For the lower values of shell length the graph is almost parallel to the horizontal axis and the gradual upward slope does not begin until a shell length of about 8·0 mm. is reached. It has already been shown that this change is brought about by the onset of the adult phase and it should be noted that it occurs at a greater shell length in the Sierra Leone population than

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FIGS. 31–35. Stages in the development of the accessory genital glands and male copulatory organ of *B. jousseaumei* from the Gambia.

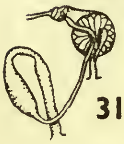
Fig. 31 at 4·5 mm. shell length.
Fig. 32 at 5·2 mm. shell length.
Fig. 33 at 6·3 mm. shell length.
Fig. 34 at 7·5 mm. shell length.
Fig. 35 at 8·8 mm. shell length.

FIGS. 36–38. Stages in the development of the accessory genital glands and male copulatory organ of *B. globosus* from Sierra Leone.

Fig. 36 at 6·1 mm. shell length.
Fig. 37 at 8·5 mm. shell length.
Fig. 38 at 9·2 mm. shell length.

FIGS. 39–41. Similar stages in *B. globosus* from Angola.

Fig. 39 at 8·9 mm. shell length.
Fig. 50 at 9·5 mm. shell length.
Fig. 41 at 9·75 mm. shell length.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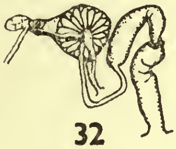
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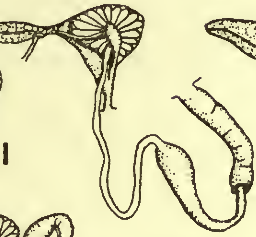
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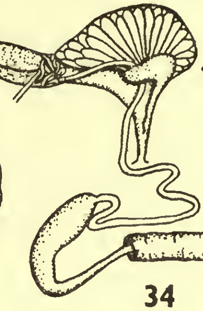
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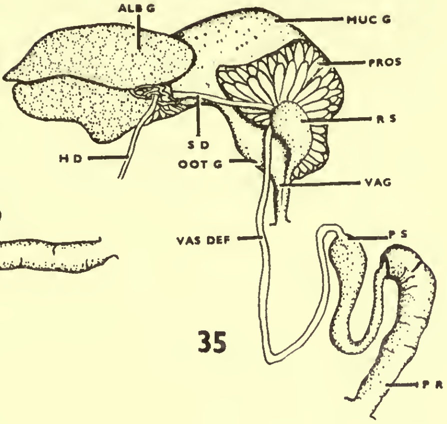
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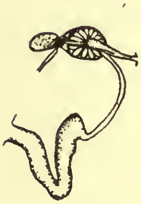
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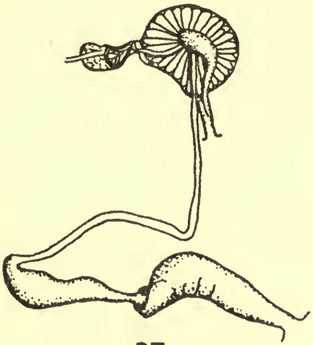
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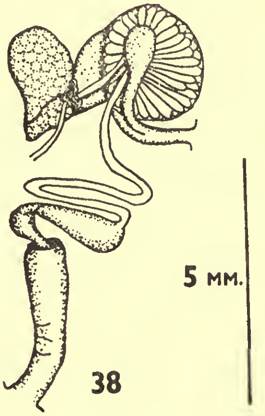

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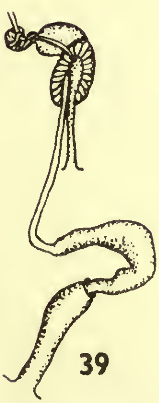
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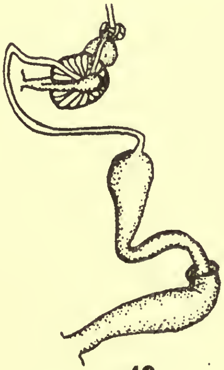
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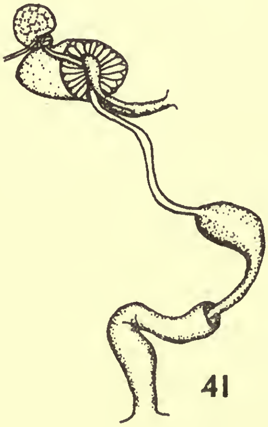
41

in that from the Gambia. That the same characteristic is present in the corresponding graph for the Belgian Congo material is almost certain ; the distribution of individuals in the sample is, however, such that the feature is not well marked although it seems probable that it occurs at an even greater size than in the Sierra Leone population.

Although no anatomical differences in structure have been found in the limited material examined (Sierra Leone, Belgian Congo and Angola) there is a variation in degree of development of the genital organs at corresponding shell sizes. Text-figs. 31–35 show stages in the development of the accessory genital glands and male copulatory organ at various shell lengths for *B. jousseaumei* in the Gambia. Text-figs. 36–38 are of three stages in *B. globosus* from Sierra Leone and Text-figs. 39–41 for material from Angola. The degree of development of the Gambian specimen of 5·2 mm. shell length (Text-fig. 32) compares well with that of 8·5 mm. from Sierra Leone (Text-fig. 37) and 9·5 mm. from Angola (Text-fig. 40). The protandrous development of the male copulatory organ and prostate is even better marked in these last two groups of specimens than it is in *B. jousseaumei.*

Of possible significance, but at present insufficiently investigated, is the increased pigmentation of the mantle in the more southern forms. Specimens from Sierra Leone and the Belgian Congo have the mantle heavily blotched with black in contrast to the more diffuse spotting of that in *B. jousseaumei.* Three of the four specimens dissected from Angola had almost the entire mantle black with one or two lighter patches.

Differences in the radula do not seem significant ; one or two more laterals in each transverse half row may be found in the larger forms but this is to be expected.

DISCUSSION

Evidence has been presented to show that *Bulinus jousseaumei* from the Senegambian region is closely related to the other species of the sub-genus *Physopsis* from neighbouring West African territories and that these in turn are related to the typical *Bulinus globosus.* In spite of a number of distributional gaps, probably due to an absence of collectors rather than of snails, it seems clear that there is a well-marked cline grading from the typical *globosus* form in the south to the small *jousseaumei* at the extreme northern limit of the range. Not only is this cline represented by a gradation in size but also by a gradation in the degree of protandric development, possibly also by differences in the intensity of mantle markings. The change does not become really well marked until (moving northward) Sierra Leone is reached. It seems very probable that the cline is correlated with the length of the rainy season. In the Senegambian region there is a single wet season of about four months duration while to the south the season is prolonged and may be duplicated. The short single wet season will limit the time during which the streams and bolons are suitable for the development of snails, hence the telescoping of the sexual phases and the reaching of sexual maturity at a smaller shell size. In regions of more continuous rainfall the need for rapid development is less, resulting in the more marked protandrous development (a primitive character) and the later onset of sexual maturity, the latter being of course closely connected with the larger shell size.

Although the use of a trinomial system of nomenclature is of doubtful value unless it is well documented it seems justifiable to retain the name *jousseaumei* as a sub-species in this case, for the Senegambian form. It differs from the typical form of *globosus* in its considerably smaller size and its apparently more contracted life cycle. It is at present geographically isolated from the typical form by the distributional gap in Portuguese Guinea but subsequent work may well show that this is not actually so. The name *Bulinus* (*Physopsis*) *globosus jousseaumei* (Dautzenberg) is therefore proposed.

If *B. jousseaumei* is a sub-species of *B. globosus* then the problem of its affinities with the strongly umbilicate form of *B. globosus* described from the Gambia (Wright, 1956) arises since two geographical races of the same species are not to be expected in the same geographical region. In this form the columellar margin of the aperture is greatly developed and not reflected, giving rise to a wide umbilicus with a slight keel around its opening. The columellar truncation is also thus suppressed leaving only a thickened line on the inner surface of the columella. There appears to be no record in the literature that the type series of *B. globosus* includes several specimens which show this character in a very limited degree. Material in a collection made in Northern Rhodesia by Dr. P. Le Roux contains a number of specimens which show this character even further developed. Intermediate forms between the Rhodesian and Gambian specimens have been seen in Blacklock's collection from Sierra Leone. In these the umbilicus is well developed but not quite so wide as in the Gambian material. Although the evidence is incomplete it appears that this variety of *B. globosus* also shows a clinal distribution parallel to that described for the typical form and *B. jousseaumei*. In this instance the main character in which gradation has been observed is in the degree of overgrowth of the columellar margin with consequent suppression of the columellar truncation and increase in the size of the umbilicus. Insufficient spirit material has been available for a study of associated anatomical variation. The only locality from which this umbilicate form was obtained in the Gambia was at Badja Kunda, Upper River Division where the ecological conditions differed slightly from those in the typical *B. jousseaumei* habitats. A single specimen of *B. jousseaumei* showing this character slightly developed was obtained with normal specimens at Sudowol bridge over the Simoto bolon, Upper River Division. The evidence suggests that this is possibly a recessive genetic character of the normal form which, when it occurs as a pure homozygous population is better adapted to slightly different habitats and appears to behave as a separate species.

SUMMARY

1. A brief biometrical study of the shell of *B. jousseaumei* is made.

2. The histology and course of development of the genital tract of this snail is described and compared with related planorbids.

3. The records of *Physopsis* spp. from West Africa are briefly surveyed. The possibly fallacious premises on which *Bulinus globosus ugandae* Mandahl-Barth

was described are mentioned and *Bulinus hemprichii depressus* Haas is referred to the synonymy of *B. globosus*.

4. The relationship of *B. jousseaumei* to *B. globosus* is discussed and the former is reduced to a sub-species of the latter as *B. g. jousseaumei*, the northernmost representative of a cline of the typical form.

5. The relationship of *B. g. jousseaumei* to the umbilicate form of *B. globosus* is discussed and this form is related through a graded series to the typical form.

ACKNOWLEDGMENTS

In addition to acknowledgments made in the text I am greatly indebted to Dr. T. P. Eddy, Director of Medical Services, Sierra Leone, and to Dr. J. Schwetz of Brussels, both of whom have sent to me useful material from Sierra Leone and the Belgian Congo respectively ; also to Dr. John Morton who has been kind enough to read the manuscript and make a number of useful suggestions. My thanks are also due to the Director of the Institut Royal des Sciences Naturelles de Belgique both for the photograph of the type specimens of *Isidora jousseaumei* and for permission to publish this photograph.

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ABBREVIATIONS USED IN FIGURES

FIGS. 5 &6.—

BUC = buccal ganglion.
CER = cerebral ganglion.
OT = otocyst.
OT N = otocyst nerve.
PED = pedal ganglion.
PEN N = penial nerve.
PL = pleural ganglion.
VIS = visceral ganglion.

FIG. 7.—

CAE = caecum.
CRO = crop.
GIZ = gizzard.
INT = intestine.
STO = stomach.

FIG. 35.—

ALB G = albumen gland.
H D = hermaphrodite duct.
MUC G = muciparous gland.
OOT G = oöthecal gland.
P R = preputium.
PROS = prostate.
P S = penis sheath.
R S = receptaculum seminis.
S D = sperm duct.
VAG = vagina.
VAS DEF = vas deferens.

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PLATE 1

Top row: *Bulinus* (*Physopsis*) *globosus jousseaumei* from Upper River Division, Gambia (× 2.)

2nd row: *B.* (*P.*) *globosus jousseaumei* from Casamance Province, Senegal. (× 2.)

3rd row: *B.* (*P.*) *globosus* from French Guinea. (× 2.)

4th row: *B.* (*P.*) *globosus* from Kailahun District, Sierra Leone. (× 2.)

5th row: *B.* (*P.*) *globosus* from Bolahun, Liberia. (× 2.)

6th row: *B.* (*P.*) *globosus* from Kongola, Belgian Congo. (× 2.)

7th row: *B.* (*P.*) *globosus* from Angola, specimens from type series. (× 2.)

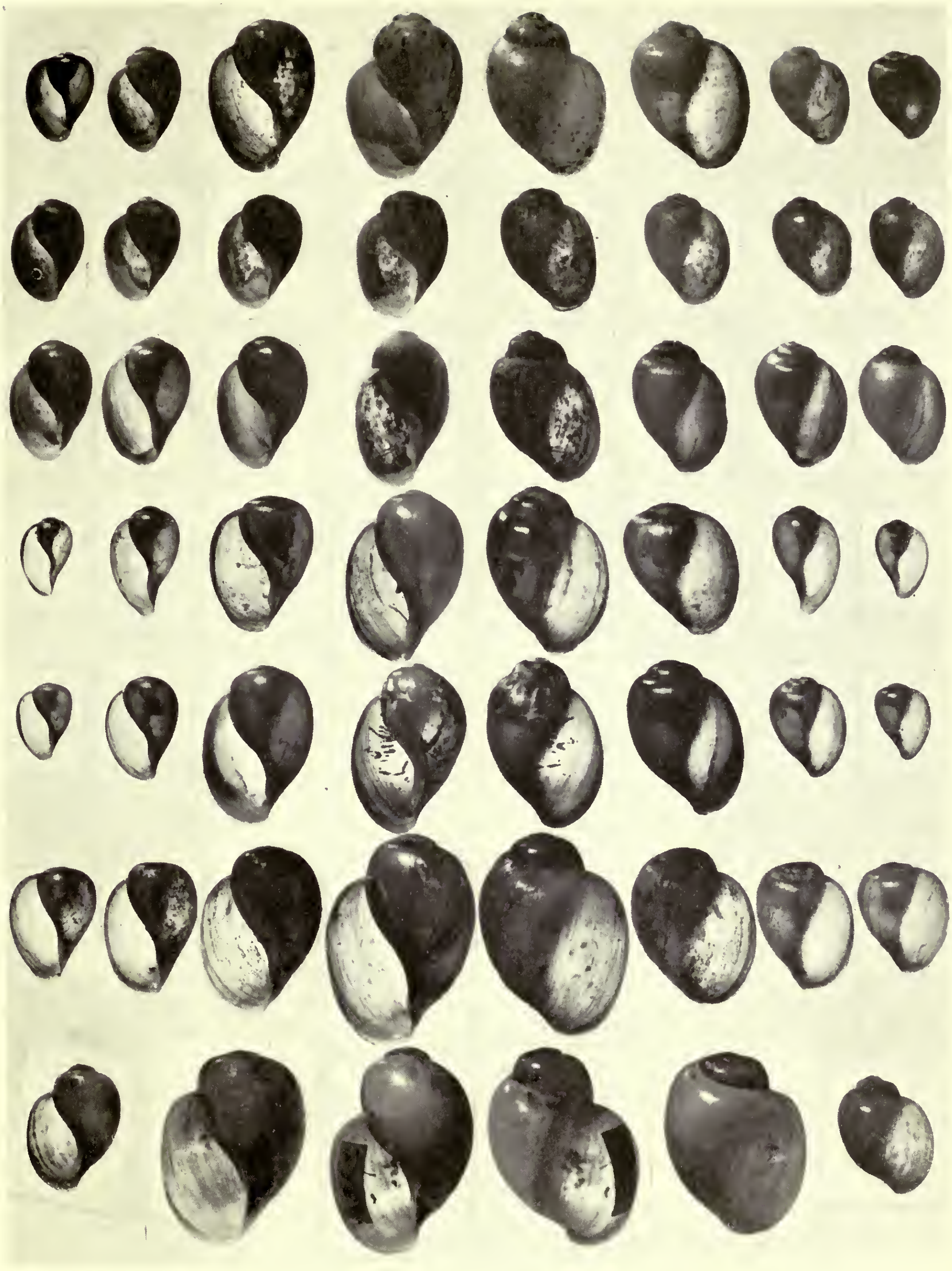


PLATE 2

Top row : Figured type specimens of *Isidora jousseaumei* Dautzenberg. (× 1·5.)

2nd row : Umbilicate form of *Bulinus* (*Physopsis*) *globosus* from the Gambia. (× 2.)

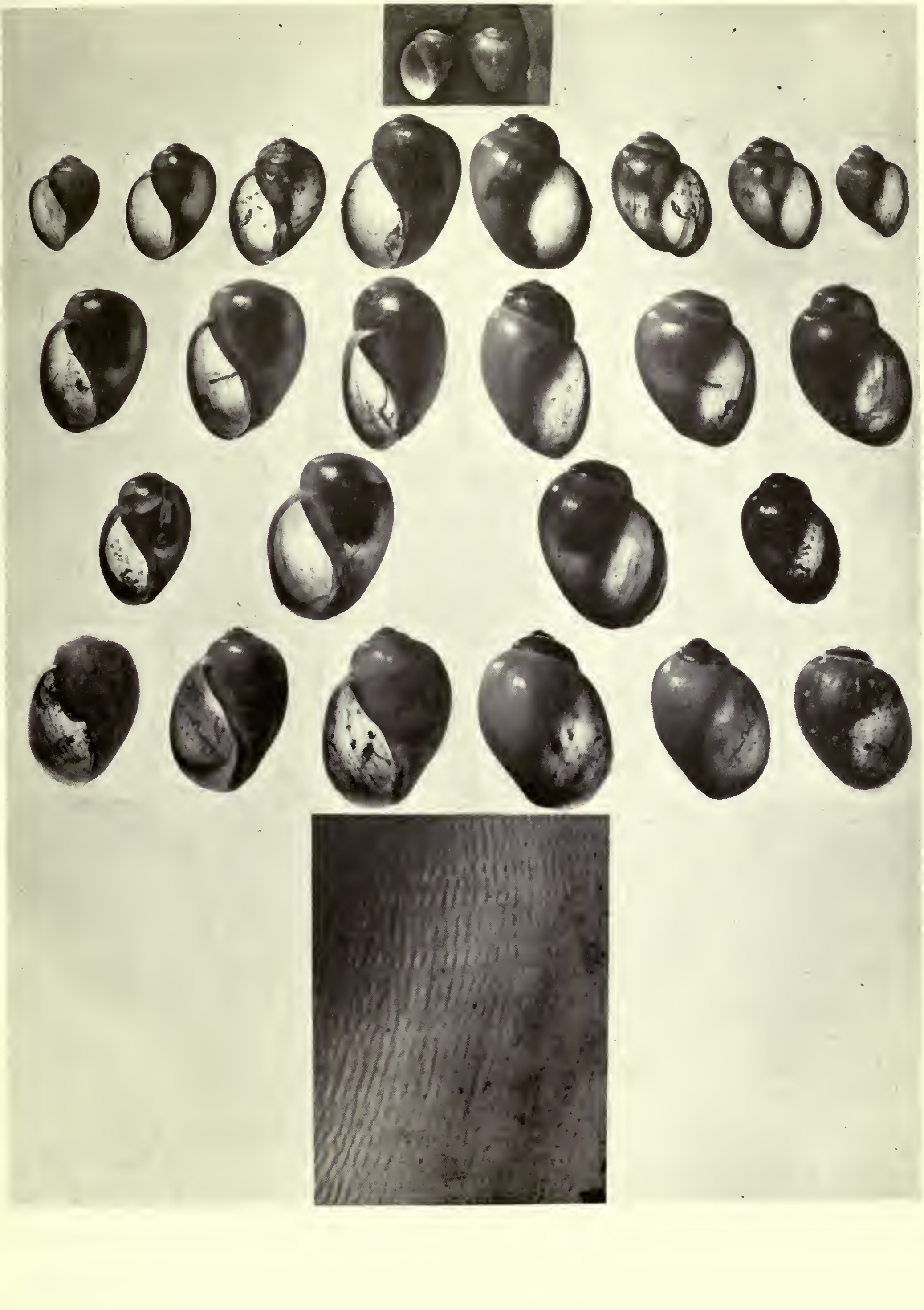
3rd row : Umbilicate form of *B.* (*P.*) *globosus* from Sierra Leone. (× 2.)

4th row : Umbilicate form of *B.* (*P.*) *globosus* from Northern Rhodesia. (× 2.)

5th row : Umbilicate form of *B.* (*P.*) *globosus* from Angola, specimens from type series. (× 2.)

Bottom : High-power view of micro-sculpture on shell of *B.* (*P.*) *globosus* from Sierra Leone

PLATE 2.



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ON *SPELAEOGRIPHUS*, A NEW CAVERNICOLOUS CRUSTACEAN FROM SOUTH AFRICA

ISABELLA GORDON

BULLETIN OF
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ZOOLOGY Vol. 5 No. 2

LONDON: 1957

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Pp. 29–47 ; 26 *Text-figures*

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical Series.*

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Issued March 1957 *Price Six Shillings*

ON *SPELAEOGRIPHUS*, A NEW CAVERNICOLOUS CRUSTACEAN FROM SOUTH AFRICA

By ISABELLA GORDON, D.Sc., Ph.D.

SYNOPSIS

A new cavernicolous Malacostracan from a pool in a cave on Table Mountain, *Spelaeogriphus lepidops* n.g. and sp., is described and figured. The affinities of the genus are discussed. In some respects it resembles *Monodella* (Thermosbaenacea), in others it approaches the Anaspidacea (Syncarida), or the Tanaidacea (Peracarida), but it is not referable to any of these Orders. Specimens received later included an ovigerous female carrying ten to twelve large ova in a characteristic Peracaridan brood-pouch composed of five pairs of oostegites. The genus, therefore, belongs to the Division Peracarida and, as it is not referable to any of the existing Orders of that Division, is placed in a new Order Spelaeogriphacea and a new family Spelaeogriphidae each with the characters of the genus. Nothing is known of the internal anatomy or of the embryology.

INTRODUCTION

Recently members of the South African Spelaeological Association obtained some specimens of a small blind Malacostracan from a pool at a depth of 110 ft. in a cave on Table Mountain, South Africa. The animals were said to " swim swiftly with rapid undulations of the body ". The temperature of the water in which they lived was 50° F. (February, 1956).

The specimens were submitted to Dr. K. H. Barnard who found that they represented a new genus and species of Crustacea Malacostraca which at first sight seemed referable to the Division Syncarida but on closer examination seemed rather to belong to the Peracarida—its " affinities seem to be with the Tanaidacea, especially *Apseudes* " to quote from Dr. Barnard's letter. In April 1956 Barnard sent to the British Museum six of the specimens, together with notes and sketches, and suggested that I might like to describe this interesting new species and discuss its affinities in more detail. I wish to express my thanks to Dr. Barnard for presenting these specimens to the Museum and also for the privilege of studying them.

The specimens were sent to London in two small vials. One vial contained two almost-perfect specimens which are quite opaque and much better preserved than the other four ; these have been selected as the holotype, a male measuring 7·2 mm. in length (from tip of rostrum to posterior margin of telson) and the allotype, a female measuring 5·6 mm., respectively. The four paratypes are very delicate, almost transparent, and more or less imperfect as to their appendages ; they range from 4·9 to 6·8 mm. in length and comprise two females and two males (one rather immature). The holotype and allotype have been handled with care and, for the necessary dissection, the more incomplete paratypes have been used. Some specimens have been retained for the South African Museum collection and according to Barnard the largest measures 7·5 mm. in length.

The name suggested by Barnard for this new genus was most appropriate but, unfortunately, it is now preoccupied by *Spelaeocaris* Matjašič (1956, p. 65) a new genus of the family Atyidae. I therefore propose the name *Spelaeogriphus* from " griphos " meaning something complicated, a puzzle or riddle, not " gryphos " meaning a griffin (Jaeger, 1955).

Spelaeogriphus n. g.

Diagnosis. Body elongated, subcylindrical (somewhat depressed). Carapace short, deep, coalescing dorsally with first thoracic somite and overhanging on each side to largely conceal the mouthparts and to enclose a branchial cavity within which lies the large, pedunculate, cup-like epipodite of the first thoracic limb (maxilliped). Each lateral flap of carapace deeply separated anteriorly from the dorsal part ; cervical furrow visible in the better-preserved specimens. Thoracic somites 2–8 free (although the second is almost entirely overlapped by the carapace), deepening progressively posteriorly. Abdomen long, exceeding half the total length of body ; telson distinct from the last somite. Ocular lobe oval, plate-like, movably articulated to side of rostrum, without visual elements or pigment. Antennulae almost contiguous basally, long, with two unequal or subequal flagella and a 3-segmented protopodite without statocyst but modified in the adult male. Antenna longer and more robust than antennula ; protopodite 2-segmented (peduncle therefore 4-segmented), exopodite small, scale-like, multiarticulate flagellum nearly as long as body. Mandible with lacinia mobilis, a series of 16–20 spines and a slender, 1-segmented palp. Maxillula with a slender palp near distal end of outer margin of endite 3 (broad outer lobe). Maxilla well developed ; endite 3 deeply bifurcate, each lobe with long curved apical setae ; a few stout penicillate processes on endite 2 (inner lobe). Maxilliped " Isopodan " in form, with a few retinacula on inner margin of inner plate (endite of basipodite) a 5-segmented palp, no exopodite, a large respiratory cup-like epipodite. Lower lip without movably articulated apical lappets. Peraeopods simple, ambulatory, none markedly modified ; epipodites absent ; exopodites present on 1–6 (a rudiment on 7 is exceptional). Three anterior pairs of exopodites 2 (3)-segmented, setose, natatory ; three posterior pairs 1 (2)-segmented, non-setose, respiratory (gills). Pleopods alike in both sexes ; first four pairs well-developed, biramous, natatory, fifth pair vestigial. Uropods broad, biramous ; exopodite 2-, endopodite 1-segmented. A simple penial process on coxopodite of peraeopod 7 in male ; incipient oostegites on peraeopods 2–5 in female (not mature). In a more mature female sent after this paper was completed oostegites are present on peraeopods 1–5 inclusive (see p. 44).

Nothing is known of the internal anatomy or of the development.

Gender of genus : masculine. Genotype : *Spelaeogriphus lepidops* n. sp.

Holotype, allotype and the paratypes described below will be incorporated in the British Museum Collection.

Spelaeogriphus lepidops n. sp.

DESCRIPTION. The slender elongate *body* recalls that of many small cavernicolous Malacostraca ; it is subcylindrical being slightly depressed especially in the posterior third. In dorsal aspect the sides are almost parallel throughout, except posteriorly since the free telson is narrower than the abdominal and thoracic somites. In lateral aspect the body is as represented in Text-fig. 1 but the delicate side plates (pleura or epimera) of abdominal somites 1–4 are not at first glance apparent and therefore these somites appear to be less deep.

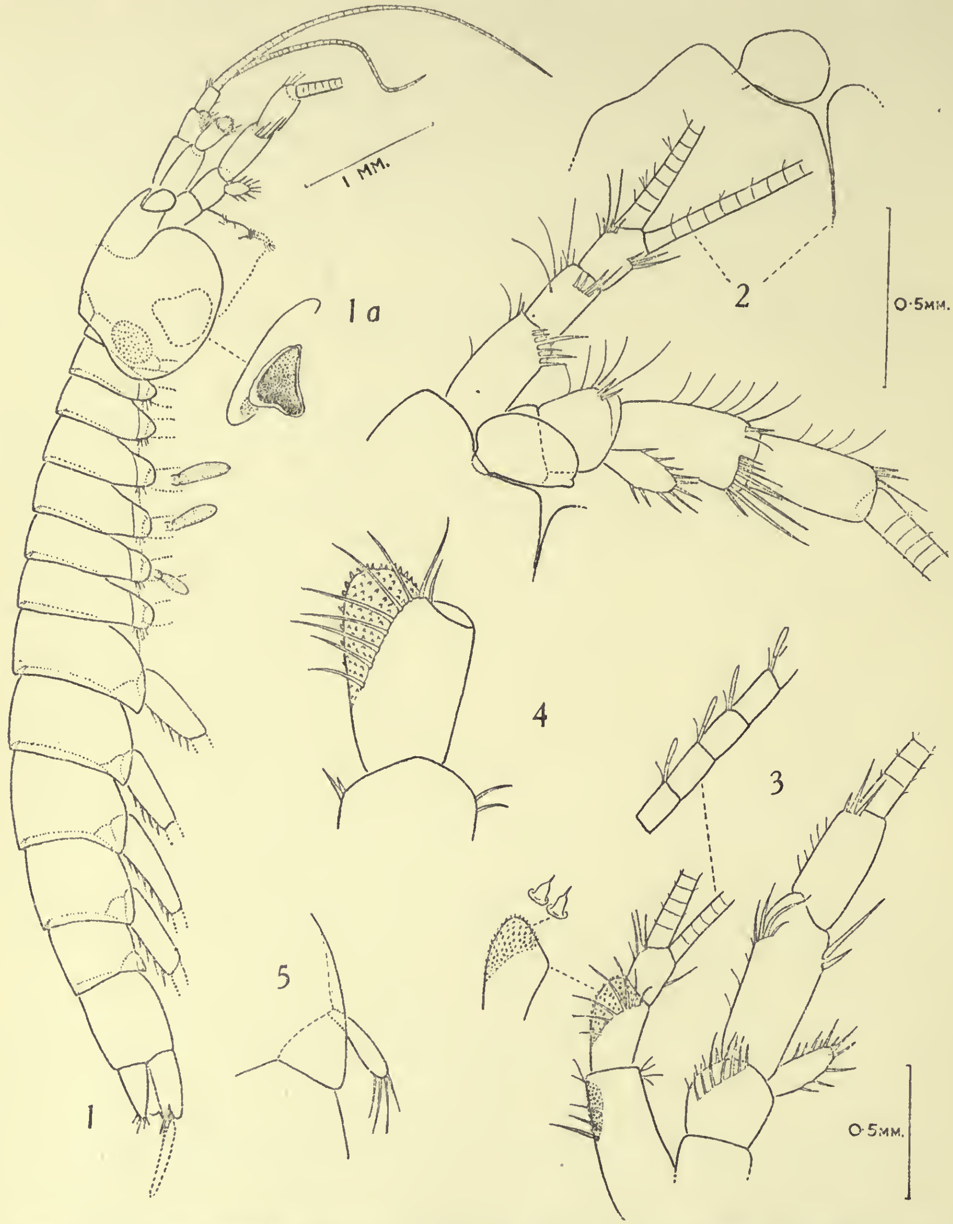
The small, distinct *carapace* is smooth except for the cervical furrow which is distinct in the holotype, but only faintly indicated in the more transparent specimens. It is produced anteriorly, between the pair of oval ocular lobes or scales, to form a somewhat depressed, broadly triangular rostrum (Text-fig. 2). In lateral aspect, the carapace is as deep as long and, in all the preserved specimens (which may be somewhat contracted), it overlaps the first free thoracic somite (number 2) leaving only a small portion exposed dorsally, and part of the third somite laterally (Text-fig. 1). Each lateral part of the anterior margin of the carapace is continued backwards, on a level with the outer rim of the ocular scale, for a considerable distance before fusing with the dorsal portion at the cervical furrow. Thus these antero-lateral flaps are doubtless capable of considerable lateral movement. Near the postero-lateral margin there is a conspicuous oval patch, above thoracic somite 2, represented by stippling in Text-fig. 1. This area, whose significance is unknown, is part of the carapace wall and can also be seen from the inside, as shown in Text-fig. 1*a*, where the ventral rim of the carapace is indicated, slightly posterior to the respiratory cup-like epipodite of the maxilliped. This large " gill " is visible through the thin wall of the carapace, but the oval patch behind it is not equally well marked in all the specimens ; for example, it is rather faint in the immature male paratype.

Thorax. The first somite is completely fused with the head region ; the second somite is free from, but almost entirely overlapped by, the carapace. Somites 3–8 become progressively deeper as represented in Text-fig. 1 although their dorsal margins are approximately equal in length.

The *abdomen* exceeds half the total length of the body. Somites 1, 2 and 5 are subequal in length and shorter than the remaining three. Somites 1–4 decrease gradually in depth but, as already mentioned, their pleura are delicate and not easy to discern. The small epimeral portion of somite 5, however, is distinct (Text-fig. 1).

The *telson* is free from, and narrower than, the sixth abdominal somite (Text-fig. 16). The median length is nearly equal to the basal width and the rounded apex bears a number of spines of varying length.

The *antennulae*, which are not widely separated from each other, are shorter and much less robust than the antennae. The proximal part of the right antennula of a female paratype is represented, in dorsal aspect, in Text-fig. 2, that of the holotype in latero-ventral aspect, in Text-fig. 3. The first segment of the protopodite, which is equal to the sum of the second and third segments, has no statocyst. In the adult male the second segment of the peduncle is modified, the distal half of the inner margin being expanded to form a lobe which is richly beset with rows of



FIGS. 1–5.—*Spelaeogriphus lepidops* n.g. and sp. Fig. 1. ♂ paratype, in lateral aspect, peraeopods omitted except for the exopodites or " gills " on 4–6 respectively. 1*a*. Ventral margin of carapace and cup-like epipodite at base of the maxilliped. Fig. 2. Lower figure—rostrum, right ocular lobe and proximal segments of antennula and antenna of a ♀ paratype, in dorsal aspect; upper figure—rostrum and right ocular lobe of the smallest paratype, an immature ♂, in dorsal aspect. Fig. 3. Proximal segments of antennula and antenna of the holotype, in ventro-lateral aspect (the segments of the protopodite are broader than shown in figure) and, at higher magnification, a few distal

conical papillae. Ventrally, this lobe is bounded by a series of long setae as shown in Text-figs. 3 and 4. There is also a small patch of the special, sharply pointed, conical papillae on the inner distal margin of the basal segment of the male peduncle. The longer flagellum comprises 40 or more segments, the smaller up to 36 segments ; in some specimens the two flagella are nearly equal in length. The distal three-fourths of the shorter (outer) flagellum has a series of short aesthetascs as shown in the enlarged portion (Text-fig. 3).

The *antennal* peduncle of a female is represented in dorsal aspect in Text-fig. 2, that of the male holotype in latero-ventral aspect and at a lower magnification, in Text-fig. 3. There is no obvious sexual dimorphism of the peduncle or protopodite. The small, scale-like exopodite bears some 10 marginal spines. The flagellum when complete is almost as long as the body and comprises about 70 segments.

The *ocular lobe* is a thin oval scale, movably articulated by means of a short peduncle to the side of the rostrum (Text-fig. 2) ; on the posterior outer edge is a tiny papilla. If viewed obliquely, the ocular scale seems to be decidedly club-shaped. There is no trace of pigment or of visual elements.

The *mouthparts* represented in Text-figs. 8–14 are, with the exception of the maxilliped (Text-fig. 13), all from the same female paratype. The upper lip, as indicated in Text-fig. 1, is deep ; the distal portion is represented in lateral aspect in Text-fig. 8. The distal portion of the left *mandible* is shown (slightly distorted by pressure of the coverslip of the micropreparation) in Text-fig. 9. The palp is reduced to one elongate segment, the molar process is well developed and the spine row comprises 16–20 graded spines. There is only very slight asymmetry of incisor process and lacinia mobilis respectively (Text-fig. 10). The robust outer lobe (endite 3) of the *maxillula* bears about 16 short apical spines and, on the distal outer margin, a slender plumose seta-like palp (Text-fig. 11) ; the rather slender inner lobe (endite 1) has three short plumose terminal papillae. The *maxilla*, together with various details at a larger magnification, is represented in Text-fig. 12 ; endite 3 is deeply bifurcate, the long curved spines on the outer lobe consist of a shaft and a slightly curved distal portion whereas those of the inner lobe have the apex bifurcate. The short inner spines of each series are somewhat conical with striate or serrulate concave (? outer) margins. Endite 2 has a few stout penicillate setae, three short and one long, on the inner margin. The *maxilliped* represented in Text-fig. 13 is from a considerably smaller specimen and, as it was not completely removed, the proximal portion (indicated by a broken line in the figure) may not be quite exact although the relative size and position of the epipodite is correct, the concavity facing inwards and forwards. The two maxillipeds are held firmly together by means of a few small retinacula on the inner margin of the inner plate (endite of the basipodite). The palp appears to be 5-segmented ; the wide second segment bears 6 stout plumose setae on the inner margin ; the third segment, which

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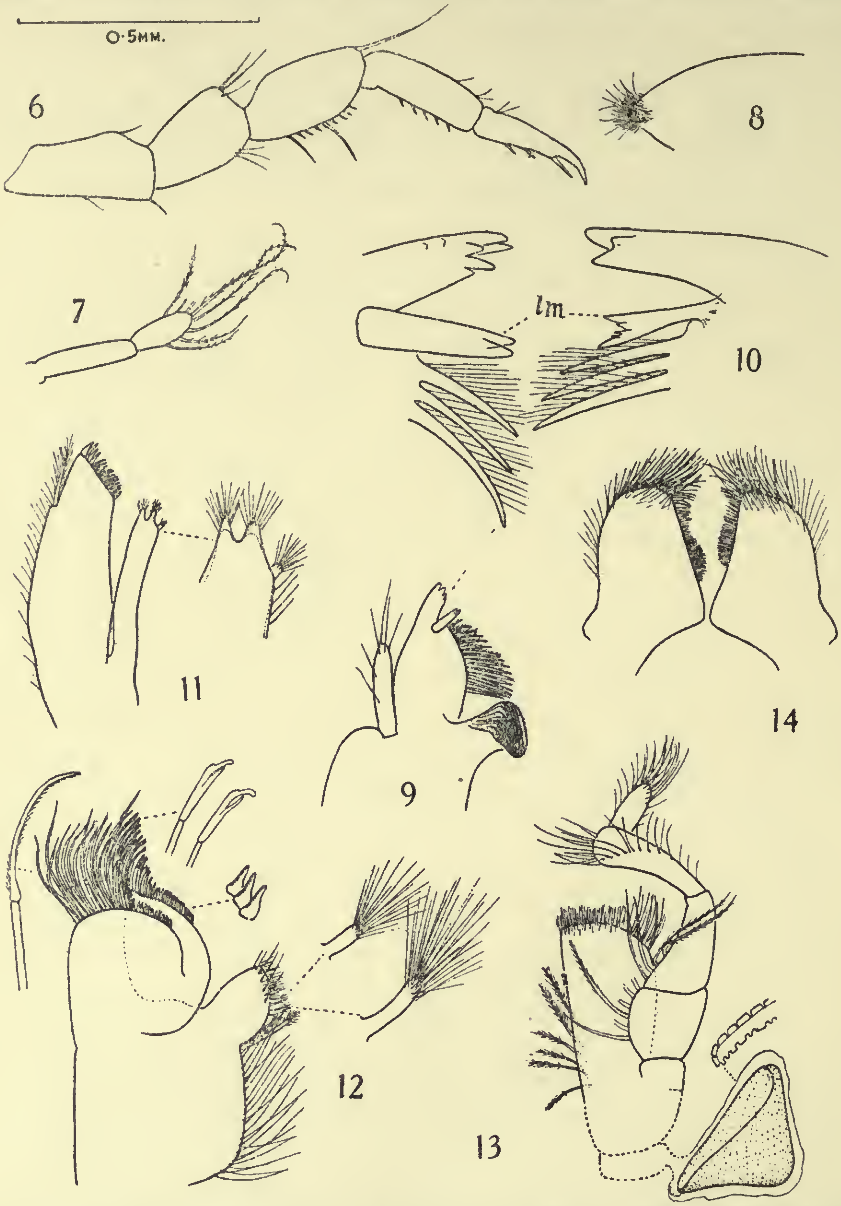
segments of the shorter antennular flagellum. Fig. 4. Second segment of antennular protopodite of ♂ paratype, in ventral aspect, to show specifically modified area beset with rows of conical papillae. Fig. 5. Vestigial pleopod 5 of ♂ paratype, highly magnified. Scale of Fig. 1 and 1*a* = 1 mm. Scale of Figs. 2 (lower) and 3 respectively = 0·5 mm.



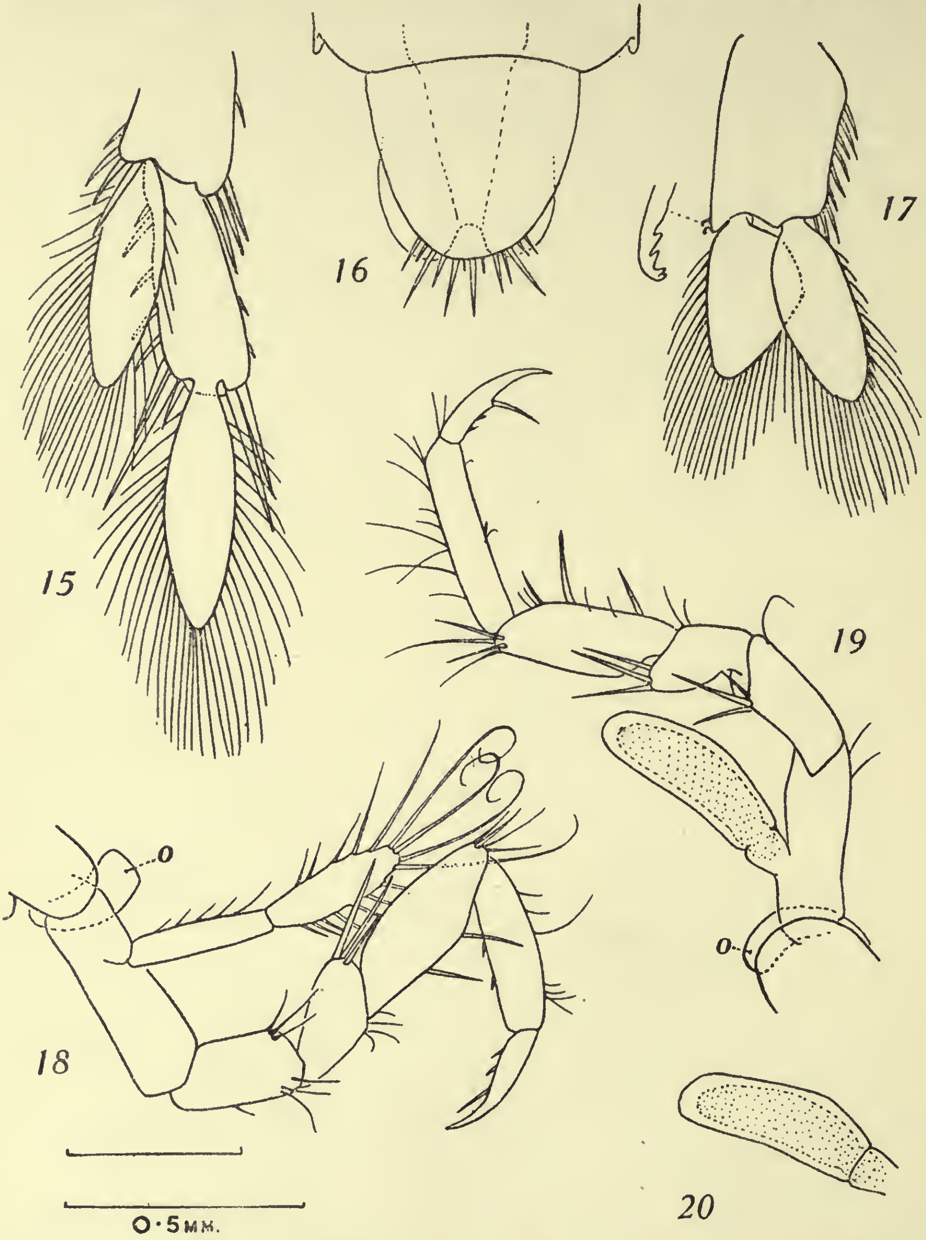
Figs. 6–14. *Spelaeogriphus lepidops* n.g. and sp. ♀ paratypes. Fig. 6. Distal segments of peraeopod 1. Fig. 7. Exopodite of peraeopod 1 of a larger specimen. Fig. 8. Upper lip, in lateral aspect. Fig. 9. Distal part of left mandible, slightly distorted by the coverslip of microslide. Fig. 10. Portion of left and right mandibles, at higher magnification, to show slight asymmetry of incisor process and lacinia mobilis. Fig. 11. Maxillula, and apex of inner lobe more highly magnified. Fig. 12. Maxilla, with enlarged details of setae and spines. Fig. 13. Maxilliped of a smaller specimen, in ventral aspect (appendage broke just below the palp; position of epipodite relative to the maxilliped is correct. Fig. 14. Lower lip. Figs. 8–12 and 14 from the same specimen. All except Fig. 10 drawn to scale = 0·5 mm.

is contracted distally, also has marginal plumose setae; the fourth segment is somewhat expanded distally and the fifth is inserted at an angle to the apex. The *lower lip*, represented in Text-fig. 14, shows no trace of the movably articulated lappet on each lobe which is characteristic of the family Apseudidae.

Peraeopods. The peraeopods, which are simple and ambulatory (pediform), are arranged in two series, an anterior one of three, and a posterior one of four, pairs as shown in Dr. Barnard's sketch (Text-fig. 26). This division is emphasized by the fact that the exopodites on each of the three anterior pairs are natatory whereas those on peraeopods 4–6 respectively are reduced and modified to serve as gills (Text-figs. 1 and 18–20). In the allotype there is also a minute gill or exopodite on the right peraeopod 7, but this is exceptional. Each natatory exopodite consists of an elongate proximal, non-setose or sparsely setose, segment and a distal segment bearing marginal setae, the apical ones being especially long and often curled; in addition a very short basal segment may be more or less clearly demarcated (Text-figs. 7, 18, 21, 24 and 25). The respiratory exopodites, the posterior of which is quite small, lack the setose terminal segment; the proximal segment is swollen and specially modified and again there is a more or less distinct small basal segment (Text-figs. 1, 19, 20 and 22).

In the adult male peraeopods 1–3 are considerably more robust than in the female or young male, but otherwise there is no sexual dimorphism. The first peraeopod is the only one which may be regarded as slightly modified; it is rather shorter than either peraeopod 2 or 3, with a smaller exopodite, a broader carpus, and more numerous spinules on the ventral margin of carpus and propodus respectively (Text-figs. 21 and 24). Text-figs. 24 and 25 represent peraeopods 1 and 3 respectively, drawn to the same scale, of the male paratype shown in Text-fig. 1; peraeopod 2 is very similar to, though a trifle shorter than, peraeopod 3. In the holotype, which is rather larger, the spine-setae on the carpus are more numerous, especially in one of the two rows (3 and 5–6, as against 2 and 2 in the paratype represented in Text-fig. 25). When the distal segments are flexed these two rows lie one on either side of the propodus. Peraeopods 4–7 are relatively more slender and increase gradually in length owing chiefly to the progressive elongation of the carpus and especially of the propodus (cf. Text-figs. 22 and 23, peraeopods 4 and 7 respectively, of a male in the South African Museum). Peraeopod 7 as a rule lacks the exopodite; a simple penial process is present in all three males on the coxopodite. This process is short in the smaller male paratype with the as yet unmodified antennular protopodite (and therefore rather immature); in the adult male it is long so that the two processes almost meet in the median line (Text-fig. 23).

The peraeopod represented in Text-fig. 6 was already detached from one of the paratypes but it probably came from one of the females; in the allotype the first peraeopod has some spinules on the ventral margin of carpus and propodus and the exopodite is shorter, especially as regards the terminal segment, than that on either peraeopod 2 or 3 (cf. Text-figs. 7 and 18). Peraeopod 4 is more slender than peraeopod 3, with a longer more slender propodus; the exopodite shows a hint of the short basal segment which, however, is distinct in that of peraeopod 5. What I consider to be incipient oostegites are present at the bases of peraeopods 2–5 but they are



FIGS. 15–20. *Spelaeogriphus lepidops* n.g. and sp. Fig. 15. Uropod of allotype. Fig. 16. Telson and posterior margin of abdominal somite 6, in dorsal aspect. Fig. 17. Fourth pleopod, with grappling hook more highly magnified. Fig. 18. Third right peraeopod of ♀ with well developed natatory exopodite and incipient oostegite *o*. Fig. 19. Fourth peraeopod with respiratory exopodite or "gill" and oostegite. Fig. 20. Detached exopodite of peraeopod 5. Figs. 16–20 from same ♀ paratype. Figs. 15 and 17 at smaller scale = 0·5 mm.; rest at larger scale = 0·5 mm.

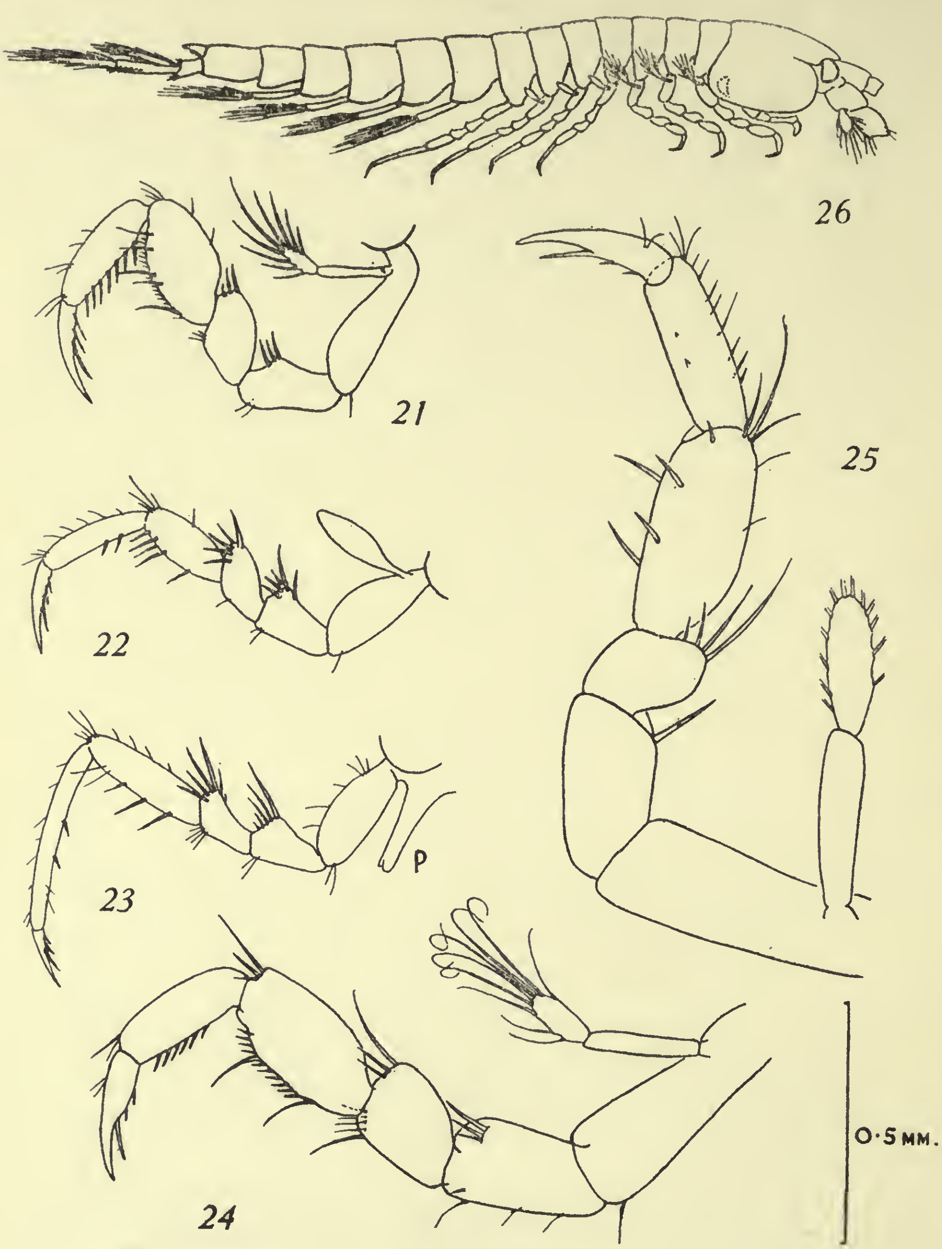
not easy to make out (Text-figs. 18 and 19, *o*). As in the male, peraeopods 5–7 lengthen progressively and the respiratory exopodite on peraeopod 6 is smaller than that on peraeopod 5. Perhaps none of the female specimens is fully mature since the oostegites are so small and inconspicuous.

Pleopods. These are alike in both sexes. The first four pairs are well developed and natatory. Each comprises a broad protopodite with two retinacula at the distal end of the inner, and a series of spines on the outer, margin and a paddle-shaped, heavily setose exopodite and endopodite (Text-fig. 17). The fifth pair is very much reduced and concealed by the small epimera of the fifth abdominal somite. In Text-fig. 5 the fifth pleopod has been displaced so that the drawing could be made, it is reduced to a slender club-shaped segment with 4 terminal setae.

The *uropods* appear to be very fragile since in none of the specimens are they now complete ; either the exopodite, or both exopodite and endopodite are as a rule missing. In the vial containing the holotype and allotype two detached but complete uropods were found. These must belong to the allotype since in the holotype the peduncles are still attached to the specimen. One of these uropods is represented in Text-fig. 15 ; the short stout protopodite is furnished with an outer and an inner cluster of apical spines ; the exopodite is 2-segmented, the proximal segment is armed with spines along the inner margin and apically—the latter spines being especially long, the distal segment is very similar in shape and size to the exopodite and both are heavily setose. In the case of the male paratype represented in Text-fig. 1 the exopodite and endopodite had apparently undergone regeneration and are smaller than is normal for the species, so in the illustration I have indicated the normal length of the endopodite by a broken line and have omitted the exopodite (which in any case is most frequently missing).

Remarks. The material available is insufficient for a study of the differences due to age and sex. Apart from that exhibited by the protopodite of the antennula (Text-figs. 2 and 3–4), sexual dimorphism appears to be slight. The segmentation of the antennular flagella is indistinct proximally, where the segments appear to be crowded, becoming more distinct distally. Dr. Barnard gives the number of segments of the flagella as about 36 and 48 respectively but this is presumably the maximum number found in the largest specimen ($l = 7{\cdot}5$ mm.). In the holotype the two flagella are not very unequal but the number of segments seems to be about 32–33 and 40–42 respectively. In the allotype the flagella are markedly unequal yet each appears to have less than 30 segments (about 24 and 28 respectively). These differences may be due to sex. In the other specimens the flagella are not always complete.

In the smallest male there is as yet no trace of the sexual modification of the first two segments of the antennular protopodite. Indeed, the antennula is relatively much shorter than in the adults, especially as regards the basal segment of the protopodite ; the smaller flagellum comprises only 15–16 segments. The larger flagellum is missing, as also are the antennae beyond the short protopodites (the two basal segments). The rostrum is also appreciably shorter than in the adults, and the ocular lobes are much more circular in outline (upper figure in Text-fig. 2).



FIGS. 21–26. *Spelaeogriphus lepidops* n.g. sp. Figs. 21, 22 and 23. Peraeopods 1, 4 and 7 respectively of a ♂ in South African Museum—sketches by Dr. K. H. Barnard; magnification not stated. Specimen probably larger than the holotype. Figs. 24 and 25. Left peraeopods 1 and 3 respectively, of ♂ paratype represented in Fig. 1. Scale = 0·5 mm. Fig. 26. Sketch of whole animal, in lateral aspect, by Dr. K. H. Barnard, showing arrangement of peraeopods in two groups, pleopods and uropod.

The first peraeopod is very similar to that of the female (Text-fig. 6) ; the others are all incomplete although in most instances the proximal segments with the well developed exopodites remain.

In a female paratype of approximately the same size as the male represented in Text-fig. 1 ($l = 6{\cdot}5$ mm.) the antennular protopodite is more slender and, especially as regards the first segment, shorter than in the male and there are fewer segments in the shorter flagellum ; the longer one is incomplete. The protopodite of the antenna is also relatively shorter and more slender (the male antennular and antennal protopodites are considerably broader than I have indicated in Text-fig. 3 where the appendages are lying obliquely, but I did not wish to risk damage to the holotype). The first three peraeopods of the male become more robust with increase in size ; in the holotype they are somewhat more robust than in the paratype from which Text-fig. 24 was obtained and Dr. Barnard's sketch is probably from a male exceeding 7 mm. in length. (Text-fig. 21).

AFFINITIES OF THE GENUS *SPELAEOGRIPHUS*

In recent years many new cavernicolous and interstitial Crustacea Malacostraca have been discovered ; these are referable for the most part to the Orders Thermosbaenacea, Bathynellacea (Syncarida), Isopoda and Amphipoda (Peracarida).

Spelaeogriphus, with its slender, elongate body, bears a striking resemblance to one of these cavernicolous forms namely, *Monodella argentarii* Stella (1951*a*, p. 2, fig. 1). But, the general similarity of telson, uropods, mandible (the palp excepted) and the exopodites[1] of the peraeopods notwithstanding, *Spelaeogriphus* is most certainly not referable to the Thermosbaenacea. This Order is unique amongst Malacostraca in the possession of a *dorsal* marsupium or brood-pouch in the female, " a chamber formed by the posterior portion of the carapace, which covers the first three somites of the body " (Stella, 1951*b*, fig. 3 of plate ; 1953, pl. 1, fig. 2). Barker exhibited some ovigerous or larvigerous females of *Thermosbaena mirabilis* Monod, with a similar dorsal marsupium, at the XIV International Congress of Zoology held in Copenhagen in 1953, but his description and figures have not so far been published (Barker, 1953). Fertilization in the Thermosbaenacea must, therefore, be internal. In *Monodella*, according to Stella (1955, p. 464), from each ovary a short duct, the vagina, leads to the base of the sixth peraeopod and another one, the oviduct, goes dorsally to the brood-pouch. The position of the vaginal openings on the seventh thoracic somite (bases of peraeopods 6) is unusual ; in Malacostraca the female genital openings are, as a general rule, on the sixth somite. Another unusual feature in *Monodella* is the presence in the male of an additional coupling organ on the maxilliped (Stella, 1955, p. 464 ; Karaman, 1953, figs. 7 and 10). These characters, together with a study of the embryology of *Monodella*, led Taramelli (1954) to exclude the Order Thermosbaenacea from the Division Peracarida and with this Siewing agrees (1956, p. 168, Diagram 3). The Thermosbaenacea have certain characters of the Syncarida, others of the Peracarida, and still others which are unique.

When Barnard first examined the specimens of *Spelaeogriphus* he thought that they belonged to the Division Syncarida. But, he writes, " further consideration shows the impossibility of including this Crustacean in that Division. Barring a superficial resemblance in having exopods on six of the peraeopods, it has none of the special features found in the Syncarida. On the contrary, its affinities seem to be with the Tanaidacea, especially *Apseudes*. The mouthparts are Isopodan in character, and the cup-like epipod on the maxilliped is clearly analogous to that found in *Apseudes* " (Barnard, in letter received 14.iv.56). After I had described *Spelaeogriphus* and had considered its possible relationships, I sent some notes and sketches to Dr. K. Lang, Director of the Stockholm Museum, since he has for some years past been engaged on a revision of the Order Tanaidacea. He replied in the following few words : " The animal you picture does not belong to the Tanaidacea but to the Anaspidacea " (letter dated 20.vii.56). Thus two eminent authorities on the lower Eumalacostraca disagree as to the systematic position of *Spelaeogriphus*.

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[1] None of these exopodites are respiratory in *Monodella*.

In my opinion *Spelaeogriphus* does not agree with either the Anaspidacea or the Tanaidacea as at present defined. In fact, like the Thermosbaenacea, it does not quite fit into either the Syncarida or the Peracarida. In Kükenthal & Krumbach's *Handbuch der Zoologie*, Zimmer (1927, p. 566) defines the Divisions of the Eumalacostraca and, as regards the external characters, *Spelaeogriphus* differs from the Syncarida and agrees with the Peracarida in having : (i) a carapace which encloses gill chambers but leaves most of the thoracic somites free ; (ii) a lacinia mobilis on the mandible ; (iii) two, not three, segments distal to the " knee " of the peraeopods ; (iv) oostegites in the female (but see later, p. 44). The antennal protopodite consists of two, not three, segments so that the peduncle comprises four segments ; this holds for some Syncarida and also (though not mentioned by Zimmer in his diagnosis on p. 566) for the Tanaidacea alone amongst the Peracarida (Calman, 1909, p. 191 ; Zimmer, 1927, p. 686). Thus there is something to be said in favour of Barnard's view that *Spelaeogriphus* is a primitive Apseudid.

On the other hand, the genus differs in quite a number of respects from Zimmer's (1927, p. 685) diagnosis of the Tanaidacea. There are seven, not six, free thoracic somites. The sides of the carapace are deep and separated anteriorly for a long distance from the dorsal or median part. The telson is distinct from, not fused with, the last abdominal somite. The abdomen itself is far longer than that of the Tanaids; but this difference may not be significant since in the Thermosbaenacea *Monodella* has a long, *Thermosbaena* a short, abdomen. The exopodites are more numerous and well developed, three pairs being natatory, three pairs respiratory ; in the Tanaidacea vestigial exopodites are sometimes present on the first two pairs of peraeopods only. While the form of the ocular lobe and of the epipodite on the maxilliped strongly recall the Apseudidae, *Spelaeogriphus* differs from that family in other respects, namely : The first peraeopods are *not* chelate or subchelate, nor is the second pair modified and fossorial. The antennulae are set closer together and are decidely smaller than the antennae. The mandibular palp is reduced to one segment, not " triarticulate " ; but this is probably of slight importance since the palp is absent in the family Tanaidae. The palp of the maxillula is *not* large and reflexed into the gill chamber, but small and placed near the distal end of endite 3 (in *Anaspides* the palp is even smaller, though more proximally placed, see

Chappuis, 1927, p. 596, fig. 584). There are no apical lappets on the lower lip. The uropods are broad, natatory whereas in Apseudids exopodite and endopodite are, as a rule, slender and multiarticulate. The Tanaidacea are entirely marine. I do not think that *Spelaeogriphus* is referable to the Order Tanaidacea, nor can it be placed in any of the other Peracaridan Orders—Cumacea, Mysidacea, Isopoda or Amphipoda.

In addition to the characters already mentioned (p. 42), *Spelaeogriphus* differs from the Anaspidacea in other respects : Epipodites are absent from all the peraeopods, whereas in Anaspidacea there are one or two on each, with the exception of the last pair. The pleopods are alike in both sexes, and the endopodite is well developed in the anterior four pairs ; in the Syncarida the endopodite is rudimentary or absent, with the exception of the first two pairs in Anaspididae and Koonungidae, in which the endopodites are modified as copulatory organs in the male (Chappuis, 1927, p. 594 ; Smith, 1909, figs 29 and 52 ; Nicholls, 1931, pl. 32, figs. 12 and 13). A thelycum or spermatheca appears to be absent in *Spelaeogriphus* but is present in Anaspidacea (Smith, 1909, fig. 27 ; Nicholls, 1931, p. 476, figs A and B). There is no statocyst in *Spelaeogriphus* such as occurs in e.g. *Koonunga* (Smith, 1909, p. 502, fig. 5). Certain characters of *Spelaeogriphus*, on the other hand, do recall those of some Anaspidacea. For example, both *Spelaeogriphus* and *Koonunga* exhibit sexual dimorphism of the antennulae although the modified area in the male differs in position and in form in the two genera (c.f. Zimmer, 1927, p. 595, fig. 580 with Text-fig. 3 of the present paper). The three pairs of respiratory exopodites on peraeopods 4 to 6 in *Spelaeogriphus* are unusual—they resemble epipodites but from their position on the limbs both Barnard and I think they must be exopodites. The only other Eumalacostraca with exopodites of this type are Syncarida ; in the Anaspididae peraeopod 6 (thoracic limb 7) bears, in addition to the two epipodites, a reduced respiratory exopodite, whereas those on the anterior peraeopods are long and multiarticulate (Smith, 1909, p. 516, fig. 24 and p. 513, fig, 21). The free second thoracic somite, free telson and broad uropod recall the Anaspidacea and in *Koonunga* there is a distinct V-shaped notch above the attachment of the antenna in the frontal margin of the cephalon (Sayce, 1908, pl. 1, figs. 1 and 3) ; in *Spelaeogriphus* there is a long slit in this position (Text-figs. 1, 2). It is possible to imagine a Syncarid *with* a carapace since, in the Division Peracarida, the carapace is present or absent and, when present, varies greatly in relative size. According to Barnard the mouthparts are Isopodan in character but the maxillula is not unlike that of Anaspidacea, especially the position and direction of the palp (Sayce, 1908, pl. 1, fig. 12 ; Smith, 1909, p. 508, figs. 13, 14). In the Anaspididae the mandible shows a hint of bifurcating although there is no lacinia mobilis, and the proximal epipodite on the maxilliped is large although not cup-like (Smith, 1909, figs. 9, 10 and 19). If *Spelaeogriphus* is a Syncarid it certainly is not referable to either the Anaspididae or the Koonungidae. Nor can it be placed with the minute rather degenerate members of the Bathynellidae although, if Uéno's observations are correct, some species of this family would seem to possess oostegites. Dr. Chappuis, whom I consulted on this point, writes " No! there is no brood pouch in *Bathynella* or *Parabathynella* ; the eggs are laid one after the other just where the animal happens to be " (letter dated 22.v.26). Yet Miuri and Morimoto (1953, p. 239) say of *Bathynella morimotoi* Uéno " Adult females carrying eggs and newly-hatched larvae are obtainable at all seasons of the year ". In the following year Uéno (1954, p. 525, fig. 3*b*) figures a long elliptical lamella on the coxopodite of the second peraeopod of *Bathynella inlandica* n. sp. and says that these structures, which are also present on the first pair of peraeopods, are presumably oostegites (marsupium). Here then is a Peracaridan character in certain species of the Bathynellacea.

Like the Thermosbaenacea, *Spelaeogriphus* possesses certain characters of the Syncarida, others of the Peracarida. For the present it seems advisable to refer it to a new family, Spelaeogriphidae, with the characters of the genus, and to leave the systematic position of the family as uncertain. Perhaps when the internal anatomy and the embryology of *Spelaeogriphus* are known the systematic position of the family will be elucidated. As new forms of primitive Eumalacostraca come to light it may be necessary to revise the classification and even to redefine the major Divisions.

ADDITIONAL NOTE

After the manuscript was finished I received from Dr. Barnard two further specimens accompanied by the following note : " New species of shrimp ; pair found copulating. Bats Cave, stream at bottom. Collected by S.A.S.A. 29.7.56." The male and female were thought to be copulating when caught, and each should therefore be sexually mature. Unfortunately, uropods, antennulae and antennae are incomplete in both and in the male the posterior two or three peraeopods are broken and most of the gill-like epipodites are missing.

In the male, which measures 6·5 mm. in length, the modified lobe on segment 2 of the antennular protopodite is more pronounced distally than that represented in Text-fig. 4 and the conical papillae extend almost to the proximal articulation of the segment ; the patch on the inner distal margin of segment 1 is conspicuous. There seem to be a few papillae at the inner distal angle of segment 2, and a row of 5 blunt cones on the inner margin of segment 3, of the antennal peduncle. The body of the female is slightly bent, but it appears to be rather shorter and is more slender than that of the male. The oostegites are quite unmistakable in this specimen although they are narrower than one might expect in a breeding female. In addition to the four pairs which I detected in the type specimens, a small pair is present on peraeopods 1. The first four pairs meet or even overlap medially ; each member of the fifth pair is only about as long as wide and does not quite reach the median line.

In both specimens the peraeopods are rather bunched together and each is flexed towards its partner. Barnard sketches the peraeopods as arranged in two series, 1–3 directed forwards and 4–7 directed backwards (Text-fig. 26) and in life this may be the case.

There can now be no doubt as to the presence of a ventral thoracic marsupium such as is characteristic of the Division Peracarida. *Spelaeogriphus*, therefore, seems referable to that Division and, as far as the external characters are concerned, it agrees with the definition of the Peracarida given by Calman (1909, p. 149) and also that given by Zimmer (1927, p. 566) if very slightly modified to read " . . . Antennenstamm 2- oder 3-gliederig." (As already mentioned, Zimmer failed to recall that the antennal protopodite of the Tanaidacea is only 2-segmented, although he does mention this in his treatment of the Order on p. 686). However, the family Spelaeogriphidae cannot be placed in the Order Tanaidacea for reasons which I have already given (p. 42). Nor can it be placed in any of the other Peracaridan Orders although the elongated abdomen and free telson, the large number of exopodites, and the sexual modification of the antennula in the male are characters which it shares with the Mysidacea. The only alternative, therefore, is to establish a new Order Spelaeogriphacea, with the characters of the family, to receive it.

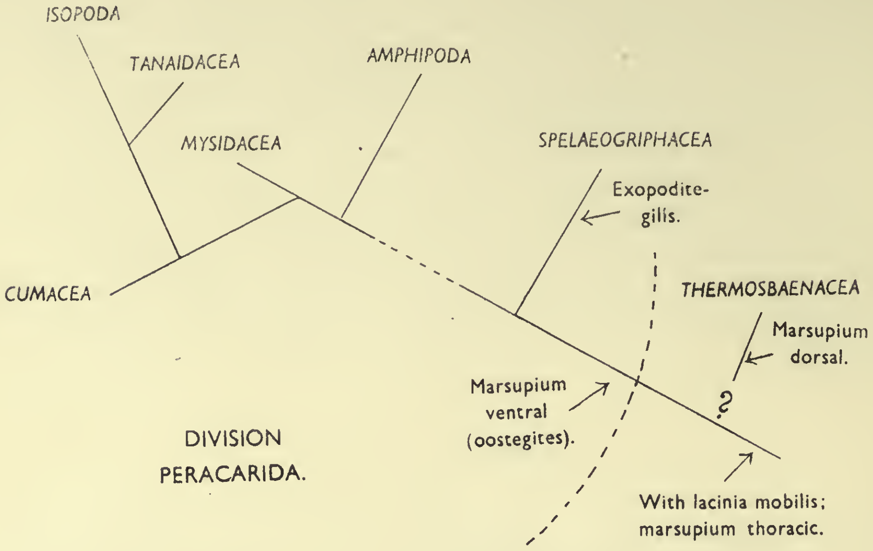
It is to be hoped that ovigerous females and larval stages may soon be collected and also that specimens fixed in Bouin or another suitable fixative will be available for sectioning.

POSTSCRIPT 18.xii.56.

After the manuscript had gone to press I received five additional specimens collected in Bats Cave, on 9.ix.56 by the S.A.S.A. One of these is an ovigerous female with a relatively large brood-pouch containing about 10–12 large ova ; the outlines of the separate oostegites are not clearly distinguishable but it is a normal Peracaridan brood-pouch composed, as already stated, of five pairs of oostegites on peraeopods 1–5 (somites 2–6).

I also sent tracings of the illustrations to Dr. Rolf Siewing of Kiel, who has done some excellent work on the comparative morphology of the Crustacean Malacostraca. He replied as follows : " Mit grosser Freude habe ich Ihre Zeichnungen von *Spelaeogriphus lepidops* studiert. Der neue Fund hat mich sehr interessiert . . . Meine Meinung nun zu der Neuentdeckung ist, dass es sich nicht um einen Vertreter der Syncarida handelt. Es fehlen bei *Spelaeogriphus* Epipodite, die bei den Syncarida wenigstens an einigen Thorakalextremitäten ausgebildet sind. Ein freier Carapax ist bei den Syncarida ebenfalls niemals ausgebildet. Die Oostegite und die Lacinia mobilis sind aber ganz typische Charakteristica der Division Peracarida. Ich halte es nicht für wahrscheinlich, dass sich diesse Organe unabgehängig in einer anderen Kategorie der Malacostraca noch einmal entwickelt haben. Auffällig sind aber manche Übereinstimmungen mit den Thermosbaenacea : Bau der Extremitäten des Thorax, Carapax, und Lacininia mobilis der Mandibel. Möglicherweisse ist *Spelaeogriphus* mit ihnen näher verwandt und stellt ein primitives Bindeglied dar. Sicher wird die Untersuchung der inneren Anatomie weitere Aufschlüsse geben."

I too had been much impressed by the resemblances between *Spelaeogriphus* and *Monodella*—apart from the position of the marsupium, which is ventral in *Spelaeogriphus* and all the Peracarida, dorsal in the Thermosbaenacea. Dr. Siewing's comments have been most helpful and give me more confidence in proposing the new Order Spelaeogriphacea. The position of this primitive Peracaridan Order in Siewing's Diagram 3 (1956, p. 168) would appear to be within the Division Peracarida, near the suggested position of the Thermosbaenacea, thus :—


ISOPODA
TANAIDACEA
AMPHIPODA
MYSIDACEA
SPELAEOGRIPHACEA
Exopodite-gills.
CUMACEA
THERMOSBAENACEA
Marsupium dorsal.
Marsupium ventral (oostegites).
?
DIVISION PERACARIDA.
With lacinia mobilis; marsupium thoracic.

Adapted from Siewing, 1956, p. 168. Upper left-hand portion of Diagram 3.

The Thermosbaenacea and the Peracarida have a lacinia mobilis on the mandible and a thoracic brood-pouch or marsupium. The Spelaeogriphacea have three pairs of exopodites modified as gills ; this may be a secondary specialization, perhaps an adaption to the freshwater habitat, although no other cavernicolous Malacostracan possesses such gills. The relationship of the Spelaeogriphacea to the other Peracaridan Orders must, for the present, remain uncertain.

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Pp. 49–72 ; Plate 3 ; 4 Text-figures

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INTRODUCTION

In the course of rearranging the bird skeletons in the collections of the British Museum (Natural History) it seemed to me that the skeleton of *Balaeniceps rex* had more pelecaniform than ciconiiform characters. The position of *Balaeniceps* in orthodox classifications is, and nearly always has been, near the storks and herons, so that this anomalous impression of its affinities seemed to require detailed investigation. The results of this study are presented here. The skeletal characters of *Balaeniceps rex* have been reassessed in relation to stork-like and heron-like characters on the one hand, and pelican-like characters on the other.

I am grateful to Dr. H. W. Parker and to Dr. F. C. Fraser for reading the manuscript and making helpful comments, and also to Mr. J. D. Macdonald for advice and encouragement at all stages of the investigation.

HISTORICAL NOTE

There are few important original contributions to the knowledge of *Balaeniceps's* affinities. Gould, who described the bird in 1850, called it the " Grallatorial type of the Pelecanidae ", although he also noted that its external features resembled " in general contour " those of *Grus*, *Ardea* and *Cochlearius*. Jardine (1851) noted likenesses to herons in the plumage. He considered that differences from the " true " pelicans, in the nostrils, pouch, position of the laryngeal opening and the absence of webs on the feet, were sufficient to show that *Balaeniceps* was not closely related to them. Von Heuglin (1856 : 60) placed it between *Anastomus* and *Dromas* in his systematic list. Bonaparte (1855 : 143) put it in the same subfamily as *Cochlearius*, describing it as intermediate between the pelicans and the Boat-bill. Des Murs (1859 : 480) considered that the egg was like that of *Phoenicopterus*.

These were the conflicting opinions in 1860 when Parker examined the skeleton of *Balaeniceps*. He was impressed by its similarities to *Scopus* and *Cochlearius*, especially the latter, and indicated many characters which it had in common with the " Ardeine " birds. Although the storks were included in his term " Ardeine ", he seemed to stress the heron-like characters of *Balaeniceps* because he considered it to be a large edition of *Cochlearius*. He noted some similarities to the Pelecaniformes but attributed them to convergence. Bartlett's discovery (1861) of powder-down on *Balaeniceps* seemed to add weight to Parker's conclusions. Reinhardt (1860), unaware of Parker's work, found more similarities with *Scopus* than *Cochlearius* in the external characters of *Balaeniceps*, and considered that *Balaeniceps* and *Scopus* were nearer the storks than the herons. In 1861, after reading an abstract of Parker's paper, he compared a skull of *Balaeniceps* with those of *Scopus* and *Cochlearius*, but still maintained that *Balaeniceps* was related to *Scopus* and the storks. The similarities between the skulls of *Balaeniceps* and *Cochlearius* he attributed to convergence. Parker admitted (1862) that he knew nothing of the anatomy of *Scopus* when he wrote his paper, but, having seen a live *Balaeniceps*, he remained convinced of its likeness to the herons. He regarded *Ardea* as the " central type " of the storks and herons, linked to *Cochlearius* and *Scopus* by *Balaeniceps*.

These two opinions became established. Some authors agreed with Reinhardt's conclusions and placed *Balaeniceps* with *Scopus* and the storks, but most of them agreed with Parker and placed it with *Cochlearius* and the herons. Giebel (1873) showed that the pectination of the middle claw and the pterylosis of *Balaeniceps* are similar to those of *Scopus* and different from *Cochlearius*. Beddard (1888) compared the visceral anatomy with that of the storks, herons and *Scopus* and, because of the alimentary tract, powder-down patches and syrinx, concluded that *Balaeniceps* was allied to the herons. Like Beddard, Furbringer (1888) and Gadow (1893 : 137) agreed with Parker. So did Shufeldt (1901), who wrote a paper on the osteology of *Scopus* and *Balaeniceps* without having seen a skeleton of the latter.

The next important contribution was made by Chalmers Mitchell (1913) who dissected a specimen and described many more anatomical details. It is interesting that he could find no outstanding characters which indicated affinities with the herons rather than the storks, or vice-versa. He noted that *Scopus* and *Balaeniceps* had many similarities, and that they had characters common to both herons and storks. When he took each character at its face value he found *Balaeniceps* had more in common with the storks than the herons, so he decided to put it in the same suborder as *Scopus*, storks and ibises. He acknowledged that this was an arbitrary rather than a phylogenetic arrangement. He noted several similarities to the pelicans, but thought they occurred because the pelicans were related to the storks and herons.

Böhm (1930) studied the structure of the skulls of juvenile and adult *Balaeniceps*. After a comprehensive investigation he concluded that Reinhardt's, Parker's, Giebel's and his own researches showed *Balaeniceps* to be a typical stork, linking the storks to the herons. He mentioned the " outstanding relationship " between *Balaeniceps* and *Pelecanus*, but did not seem to think it significant because he thought *Pelecanus* itself was so different from the other Pelecaniformes. The only other investigations of *Balaeniceps*'s anatomy were made by Technau (1937 : 567) during his studies of the nasal cavity of birds, and by Glenny (1955 : 560) in his work on the aortic arches of birds. The former drew no conclusions as to *Balaeniceps*'s affinities, though Glenny thought it less like the Ciconiidae than is usually supposed.

After Chalmers Mitchell's contribution most authors placed *Balaeniceps* by itself in a group of equal rank with the herons and storks (e.g. Streseman, 1927–34 : 809 ; Wetmore, 1930 : 3). Mayr & Amadon (1951 : 6), however, followed Böhm's suggestion and placed it with the typical storks in the family Ciconiidae. Wetmore's classification (1951 revision) shows the generally accepted taxonomic position of *Balaeniceps* in relation to the orders Pelecaniformes and Ciconiiformes.

Order Pelecaniformes.
  Suborder Phaëthontes.
      Family Phaëthontidae.
  Suborder Pelecani.
    Superfamily Pelecanoidea.
      Family Pelecanidae.
    Superfamily Suloidea.
      Family Sulidae.
        Phalacrocoracidae.
        Anhingidae.
  Suborder Fregatae.
      Family Fregatidae.

Order Ciconiiformes.
  Suborder Ardeae.
      Family Ardeidae.
        Cochlearidae.
  Suborder Balaenicipites.
      Family Balaenicipitidae.
  Suborder Ciconiae.
    Superfamily Scopoidea.
      Family Scopidae.
    Superfamily Ciconioidea.
      Family Ciconiidae.
    Superfamily Threskiornithoidea.
      Family Threskiornithidae.
  Suborder Phoenicopteri.
      Family Phoenicopteridae.

METHODS

As the purpose of this study is to examine the pelecaniform characters of *Balaeniceps's* skeleton in relation to its ciconiiform characters, the composition of the Pelecaniformes and Ciconiiformes will be discussed to decide what *Balaeniceps* ought to be compared with.

The living members of the Pelecaniformes are apparently not very alike. Nearly every genus is placed in a separate family. From a comparison of their osteology it seems that the differences are mainly due to adaptive radiation, and that there is a well-defined basic similarity. For instance, superficially, pelicans and cormorants look less alike than storks and herons, but their skeletons have more characters in common. A possible exception is *Phaëthon*, which is peculiar in many respects and may not be closely related to the rest of the Pelecaniformes. Wetmore (1951 : 5) thinks that " the Phaëthontes possibly may have separated earlier than the Fregatae " from the pelecaniform stock. Therefore, as *Phaëthon* is atypical the Phaëthontes will not be referred to in this investigation. The Fregatae are also considered aberrant by some authors, but they have so many of the osteological characters typical of the Pelecani that they are probably fairly closely related to them.

The Ciconiiformes is basically a less uniform group than the Pelecaniformes. Osteologically, it seems to be a collection of unrelated groups which, superficially, only have long beaks, long necks and long legs in common.

The genera of the Ardeae are very alike, their outstanding variation being in size. *Cochlearius* is the most aberrant genus but, apart from its skull, it has all the characters of the typical herons. Even in its skull the heron-like characters are not completely obscured. For the present purpose, therefore, the Ardeidae and Cochlearidae will be considered together, as a monophyletic group representing the herons.

The families in the Ciconiae are not so closely related. The Scopidae, with its single monotypic genus *Scopus*, is as enigmatic in its relationships as *Balaeniceps*. The skeleton of *Scopus* is like that of a small stork in some characters, but very unlike it in others. It has often been compared with *Balaeniceps*, and most authors consider the two related. However, there is no point in comparing one genus of doubtful affinities with another, so *Scopus* will not be referred to. The Ciconiidae is probably a monophyletic group ; its genera are fairly alike, although they vary more than those of the Ardeidae. This variation mainly seems to be due to different adaptations of the beak, correlated with differences in the size and shape of the head. The third family, Threskiornithidae, appears to have much in common with the Ciconiidae, but it also has certain resemblances to the Phoenicopteri. As the affinities of the Phoenicopteri themselves are controversial it is advisable not to discuss either group until their relationships have been more fully investigated.

For the purposes of this investigation, therefore, *Balaeniceps* is compared with the suborders Pelecani and Fregatae, representing the Pelecaniformes ; the ciconiiform suborder Ardeae, representing the typical herons ; and the family Ciconiidae, representing the typical storks.

Three complete skeletons of *Balaeniceps* and three skulls were available. There was also adequate material of pelicans and their allies, frigate birds, herons and storks. The skeleton of *Balaeniceps* was systematically compared with those of *Pelecanus, Ardea* amd *Ciconia,* but other genera, especially in the Pelecaniformes, were consulted to determine the range of variation in each group.

For convenience, in the following description *Nannopterum, Halietor* and *Anhinga* will not be mentioned unless they differ from *Phalacrocorax.*

OSTEOLOGICAL CHARACTERS

A. *Skull,* see Plate 3

(1) *Premaxilla*

Of the Pelecaniformes considered here, *Pelecanus, Phalacrocorax* and *Fregata* each have a well developed hook at the tip of the premaxilla. The newly hatched chick of *Sula* also has this hook, but it decreases with age, and in the adult the tip of the premaxilla is only slightly decurved. *Anhinga* has no hook in chick or adult, but this may be an adaptation to its habit of spearing fish.

In the Ciconiidae there is no suggestion of a hook to the premaxilla in any of the genera. The nearest approach is the decurved bill of *Ibis* and *Mycteria,* but in these the distal fifth of the mandible is involved in the curvature.

The Ardeidae have straight bills. Parker (1862 : 299) argues that in *Cochlearius* a hook " certainly does exist, although feebly " but, although the tip of the rhamphotheca is decurved, it is not hooked, and the premaxilla is quite straight ventrally.

Balaeniceps has a prominent hook at the tip of the premaxilla, like the typical Pelecaniformes.

(2) *Nasal groove*

In the Pelecani and Fregatae there is a conspicuous groove running along each side of the culmen from the anterior edge of the nostril to the cutting edge of the premaxilla beside the terminal hook. This relationship of the nasal groves to the premaxillary hook is constant in *Pelecanus, Sula, Phalacrocorax* and *Fregata.* In *Anhinga* the groves are only faintly indicated.

In the Ciconiidae the nasal groves are either absent, or represented by very shallow depressions which extend from the nostrils to, at most, half-way along the beak. Both conditions are often found in the same species.

The Ardeidae have shallow depressions like those of the Ciconiidae instead of nasal grooves. In *Cochlearius* these depressions are expanded to form broad, shallow troughs, each with a ridge along the mesial border.

Balaeniceps has conspicuous nasal groves which extend from the nostril to the cutting edge of the premaxilla beside the terminal hook, exactly as they do in the Pelecani and Fregatae. The grooves are not shallow, like those of the Ardeidae and Ciconiidae, or broad like those of *Cochlearius,* but deep like those of *Pelecanus.*

(3) *Nasal septum*

In the Pelecani and Fregatae there is an ossified nasal septum. The nasal septum ot the Ciconiidae and Ardeidae is not ossified, and it is perforated in the region of the external nares. *Cochlearius* has a complete, unossified nasal septum. In *Balaeniceps* the nasal septum is ossified, as it is in the Pelecani and Fregatae.

(4) *Nasal passage*

In *Pelecanus* the external nares are vertically above, or even slightly posterior to the internal nares, and the nasal cavity lies almost vertically between them. In the other Pelecani the external nares are only slightly anterior to the internal nares. In the Ciconiidae and Ardeae the external nares are an appreciable distance anterior to the internal nares, and the nasal cavity lies obliquely between them. In *Balaeniceps* the relative positions of the nares and nasal cavity are exactly the same as they are in *Pelecanus*.

(5) *Palate* (See Fig. 1)

In the Pelecani and Fregatae the palatines are always ankylosed along the mid-line posterior to the internal nares. There is usually a median ventral ridge, more or less well developed, along the suture, with a depression for the pterygoid muscle on either side of it. These depressions extend forwards past the posterior edge of the internal narial opening only in *Fregata*. In the region of the internal nares the mesial edges of the palatines are parallel in the Pelecani, and nearly so in the Fregatae. In *Pelecanus* the ventral part of the nasal passage is divided along the mid-line by a membranous septum. There is no trace of an ossified prevomer in association with this septum, and in *Sula* the septum itself is weakly developed. The septum is better developed in *Phalacrocorax*, and in at least one species, *P. urile*, there is a thorn-like cartilaginous prevomer associated with it (unless it is carefully dissected out the prevomer is easily lost in prepared skeletons of *Phalacrocorax*). In *Fregata* the prevomer is also thorn-like, though longer and definitely ossified. The maxillopalatines vary in size throughout the Pelecani and Fregatae. In *Sula* and *Phalacrocorax* they are small and do not project beyond the palatines mesially. They are slightly larger in *Fregata*, and can be seen, in ventral view, bordering the anterior half of the internal nasal opening. In *Pelecanus* they are very large and meet in the mid-ventral line between the anterior ends of the palatines. Also in *Pelecanus*, they nearly fill the inside of the skull in the nasal region, and their posterior edges slant backwards in a straight line from the internal nares to the cranio-facial hinge. Posteriorly, the maxillopalatines do not extend past the cranio-facial hinge-line in any of the Pelecani or Fregatae.

The palatines of the Ciconiidae are not fused along the mid-line except at one point. Instead of the median ventral ridge found in the pelicans, there is a ventral crest along the mesial edge of each palatine where it borders the internal narial opening. The depressions for the pterygoid muscles extend further forward on either side of the narial opening than in *Fregata*. Immediately anterior to the internal nares the

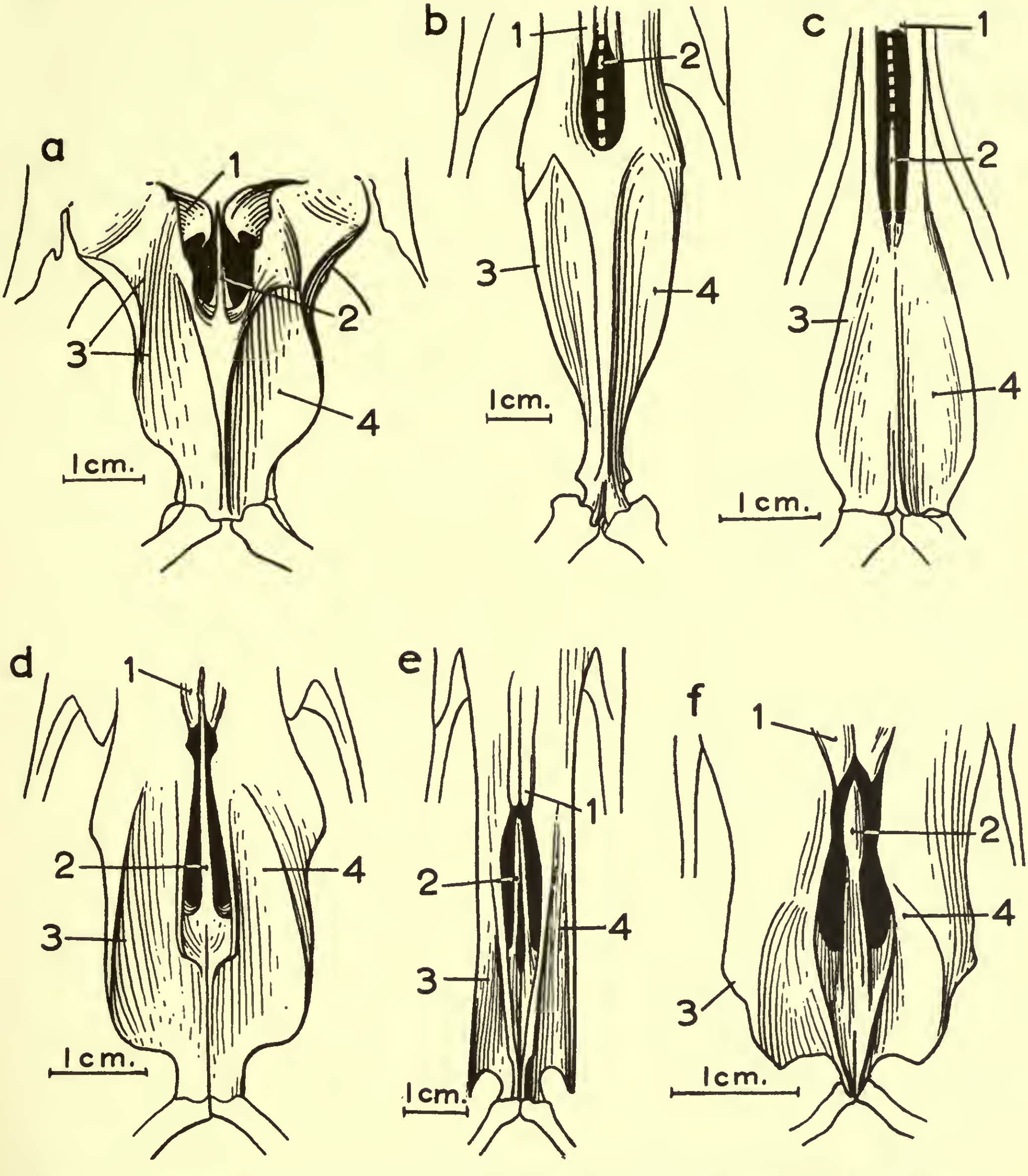

a
1
2
3
4
1cm.
b
1
2
3
4
1cm.
c
1
2
3
4
1cm.
d
1
2
3
4
1cm.
e
1
2
3
4
1cm.
f
1
2
3
4
1cm.

FIG. 1. Diagrams of ventral views of palatine regions of (a) *Balaeniceps rex*, (b) *Pelecanus crispus*, (c) *Phalacrocorax urile*, (d) *Ciconia ciconia*, (e) *Ardea goliath*, (f) *Cochlearius cochlearius*.

1 = maxillopalatine, 2 = prevomer, or position of unossified septum, 3 = palatine, 4 = depression for pterygoid muscle.

palatines approach the mid-line, and in the larger genera, such as *Leptoptilos* and *Jabiru*, they may even touch. This divides the space between them into anterior and posterior parts, the nasal passage being confined to the posterior part. The prevomer arises at the posterior end of the internal narial opening, and the palatines are ankylosed at this point. The prevomer varies from a narrow strip of bone in *Ibis*, to a substantial triangular plate, drawn out into a thin filament anteriorly, in *Leptoptilos* and the larger genera. The maxillopalatines are well developed when compared with those of most Pelecani and Fregatae. They always meet in the mid-ventral line, where they occupy most of the space between the palatines anterior to the internal nares. Each maxillopalatine is extended posteriorly into a convex projection which usually reaches beyond the cranio-facial hinge; in the Pelecani there is no such projection.

The palatines of the Ardeidae are like those of the Ciconiidae except that they are separate along the mid-line, even where the prevomer arises. In *Cochlearius*, however, they are ankylosed at this point, as they are in the Ciconiidae. The depressions for the pterygoid muscles extend as far forwards on either side of the internal narial opening as they do in the Ciconiidae. In the Ardeae, unlike the two previous groups, the vomer is V-shaped in cross-section, though this is less obvious in *Cochlearius*. The maxillopalatines meet in the mid-ventral line anterior to the nasal opening, much as they do in the Ciconiidae. Their posterior edges are convex like those of the Ciconiidae, and extend well beyond the level of the cranio-facial hinge. The maxillopalatines are smaller in *Cochlearius*, but otherwise they are very like those of the Ardeidae.

In *Balaeniceps* the palatines are ankylosed along the mid-line, posterior to the internal nares, with a broad ventral ridge along the suture. The depressions for the pterygoid muscles lie on either side of this ridge; they extend forward to the level of the nasal aperture, but no further. The condition of the palatines is thus very like that of *Pelecanus*. The prevomer is weakly developed and its degree of ossification varies in the specimens examined. It is a thin, triangular plate, often perforated, lying in a vertical plane. In some specimens the apex does not reach the anterior end of the nasal opening. This weak development of the prevomer is reminiscent of the Pelecani, in which the prevomer is reduced and sometimes missing. The maxillopalatines are strikingly like those of *Pelecanus*. Their posterior faces are flat, even concave, and not convex like those of the Ciconiidae and Ardeae (Pycraft, 1898 : 83).

(6) *Lachrymal* (See Fig. 2)

The lachrymal in the Pelecani and Fregatae descends from the frontal to the quadratojugal bar, to which it is usually attached by a ligament. Viewed posteriorly, it is a column of bone with a lateral groove, of varying depth, to accommodate the lachrymal duct. In *Phalacrocorax* a narrow lateral process of the interorbital septum meets and fuses with the ventral end of the lachyrymal. This process is larger in *Anhinga*, lying beside the lachrymal throughout its length without touching it. In lateral view, the lachrymal is more or less pillar-shaped in *Pelecanus*, *Fregata* and *Phalacrocorax*, but in *Sula* it is expanded anteriorly into the antorbital vacuity. There is a tendency, in the Pelecani and Fregatae, for this vacuity to be reduced. In *Pelecanus* it is comparatively large. In *Fregata* the maxilla grows back into it a little posteriorly. In *Phalacrocorax* there is a splint of bone resting on the quadratojugal bar. This bone fills most of the antorbital vacuity in *Anhinga*, in which the maxilla is produced posteriorly as well. The large lachrymal itself fills most of the antorbital vacuity in *Sula*, though the maxilla and the quadratojugal also expand into it.

Although the lachrymal is well developed in the larger Ciconiidae, it never reaches the quadratojugal bar. In posterior view it is roughly triangular, with the apex of the triangle downwards. In some genera, including the four largest, the lachrymal duct is wholly or partly enclosed in bone, giving a flat surface to the outer face of the lachrymal bone. Unlike the Pelecani or Fregatae, the ciconiid lachrymal has a mesial projection extending towards the interorbital septum and passing ventral to the duct of the nasal gland. The lachrymal is triangular in cross-section, and it never extends into the antorbital vacuity. This vacuity is large in the Ciconiidae, and there is no obvious tendency for the surrounding bones to expand into it.

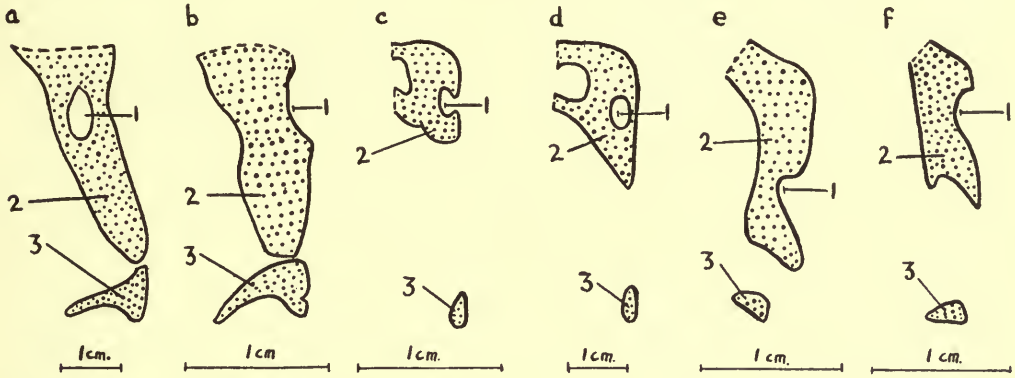


FIG. 2. Diagrammatic transverse sections of lachrymals of (a) *Balaeniceps*, (b) *Sula*, (c) *Ciconia*, (d) *Leptoptilos*, (e) *Ardea*, (f) *Cochlearius*.
1 = lachrymal duct, 2 = lachrymal bone, 3 = quadratojugal bar.

In the Ardeidae the lachrymal nearly reaches the quadratojugal bar. Its shape seems to be peculiar to the Ardeidae and is quite different from the Pelecani, Fregati and Ciconiidae. In *Cochlearius* the lachrymal is reduced, and in lateral view looks different from that of the Ardeidae ; but in cross-section it is almost identical. The antorbital vacuity is large in the Ardeidae and in *Cochlearius*.

Balaeniceps has a large lachrymal. In posterior view it is like the lachrymal of the Pelecani and Fregatae, a column of bone which meets the quadratojugal bar ventrally. The lacrymal duct lies in a large foramen through the lachrymal bone, as it does in some Ciconiidae. Anteriorly, the lachrymal fuses with the maxilla, so that the antorbital vacuity is obliterated. There is a slight groove which may represent the suture between the lachrymal and the maxilla. If it does, the lachrymal is pillar-shaped in lateral view as it is in the Pelecani and Fregatae. The complete occlusion of the antorbital vacuity, which occurs in *Balaeniceps*, is not found in any of the other groups considered here, but the Pelecani and Fregatae have a tendency towards reduction of the size of the antorbital vacuity.

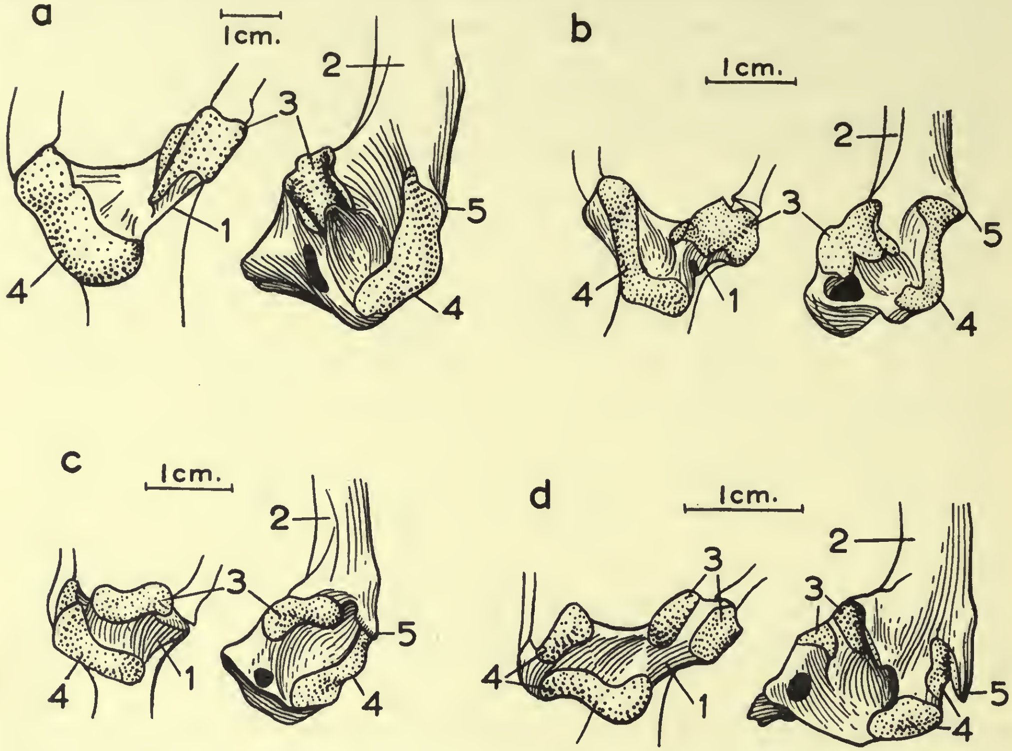


FIG. 3. Diagrams of articulating surfaces of quadrates and lower jaws of (a) *Balaeniceps rex*, (b) *Sula bassanus*, (c) *Ciconia ciconia*, (d) *Cochlearius cochlearius*.

1 = left quadrate, 2 = left ramus of lower jaw, 3 = mesial articulating facets, 4 = lateral articulating facets, 5 = lateral process.

(7) *Lower jaw articulation* (See Fig. 3)

Each of the three groups being compared with *Balaeniceps* has a different arrangement of the articulating surfaces of the quadrate and lower jaw. The arrangement is constant within each group, except that the one typical of the Ardeidae is found mainly in the larger species.

In the Pelecani and Fregatae there are two articulating facets. On the quadrate, the mesial articulation has a broad ridge, which slides in a corresponding trough in the lower jaw. The long axis of the articulation lies at an angle of about 45° to the long axis of the skull, and is in line with the long axis of the pterygoid. This is especially noticeable in *Pelecanus*. In *Sula, Fregata* and *Phalacrocorax* the lateral edge of this ridge on the quadrate is undercut, and the corresponding side of the groove in the lower jaw is overhanging. The result is a locking mechanism which, in the dried skull, is efficient enough to hold the lower jaw in place when the beak is closed. The lateral articulation is usually S-shaped, though in *Sula* it may be L-shaped. Its long axis lies approximately at right angles to that of the other articulation. In *Pelecanus*, possibly because of its wide gape, the lateral part of this articulation is modified. In the lower jaw, instead of a sigmoid articular surface there is a groove, running anteriorly, parallel to the mid-line. Along this groove slides part of the lateral articulating surface of the quadrate. This groove in the lower jaw is represented in *Sula* by a shallow transverse trough, the anterior side of which projects laterally and dorsally and lies anterior to the lateral process of the quadrate when the beak is closed. The lateral process on the lower jaw is reduced in *Fregata* and *Phalacrocorax*.

The Ciconiidae also have two articulating facets. Unlike the Pelecani and Fregatae the long axis of the mesial facet is at right angles to the long axis of the skull, and at an angle of about 120° to the pterygoid. There is no locking mechanism. The lateral articulation is curved, so that while its lateral end is at right angles to the long axis of the mesial articulation, its mesial end is parallel to it. The lateral process on the lower jaw is well developed. The relationship between the two facets is quite different from that found in the pelicans or herons, and it is very alike in all the Ciconiidae examined, whatever the relative proportions of bill and skull.

In most of the larger Ardeidae there are four articulating facets, as each of those occurring in the pelicans and storks is in two parts. The lateral part of the mesial facet and the mesial part of the lateral facet lie on a plane nearly parallel to the pterygoid. On the quadrate the mesial facet, although it is in two parts, is undercut laterally to give a locking mechanism, as it is in most of the Pelecani and Fregatae. The lateral process on the lower jaw is more prominent than in the other groups described. In *Cochlearius* the articulating facets are essentially the same as in the larger herons, but the mesial facet on the quadrate is undercut mesially as well as laterally, apparently increasing the efficiency of the locking mechanism. The lateral process on the lower jaw is even better developed than in the Ardeidae, and, with the lateral part of the lateral articulation, seems to function as an auxillary locking device.

Balaeniceps has two undivided articular facets, like the Pelecani, Fregate and Ciconiidae. On the quadrate, the mesial facet consists of a broad ridge, undercut laterally, which, in the lower jaw, slides in a trough with an overhanging lateral edge, much as it does in *Sula, Phalacrocorax* and *Fregata*. The mesial side of the trough also overhangs slightly, but not as much as in *Cochlearius*. The axis of the mesial articulation on the quadrate is in line with the pterygoid, as it is in the Pelecani and Fregatae, and is in contrast to the condition in the Ciconiidae. The lateral articulation is L-shaped, as it is in *Sula* ; its long axis is nearly at right angles to that of the mesial facet, like the Pelecani and Fregatae, and unlike the Ciconiidae. In the lower jaw, the lateral process is insignificant and the lateral articulation takes no part in the locking mechanism as it does in *Cochlearius*. *Balaeniceps* has none of the well defined ciconiid characters in its jaw articulation ; it resembles the Ardeae in some ways, but differs in others ; it is like the Pelecani and Fregatae in all the characters in which they differ from the Ciconiidae and Ardeae.

B. *Pectoral Girdle* (See Fig. 4)

(1) *Furculum*

There is a tendency in the Pelecani and Fregatae for the hypocleideum of the furculum to be fused to the keel of the sternum. The joint is ligamentous in *Phalacrocorax* ; sometimes ankylozed in *Sula* ; usually ankylosed in adults of *Pelecanus* ; and so ossified in adults of *Fregata* that the suture is obliterated. Except in *Fregata* each arm of the furculum forms an arc, convex anteriorly, between each coracoid and the carina sterni. Characteristic of the typical pelecaniform pectoral girdle is the well developed acrocoracoid flange, which forms a flat transverse surface on the clavicle for articulating with the coracoid. In *Fregata* the clavicle is completely fused to the coracoid in this region, but in young specimens the presence of the acrocoracoid flange can be inferred from the sutures. Although an acrocoracoid flange is present in several other apparently unrelated groups, it is never as well developed as it is in the Pelecani, Fregatae, *Balaeniceps* and *Scopus*.

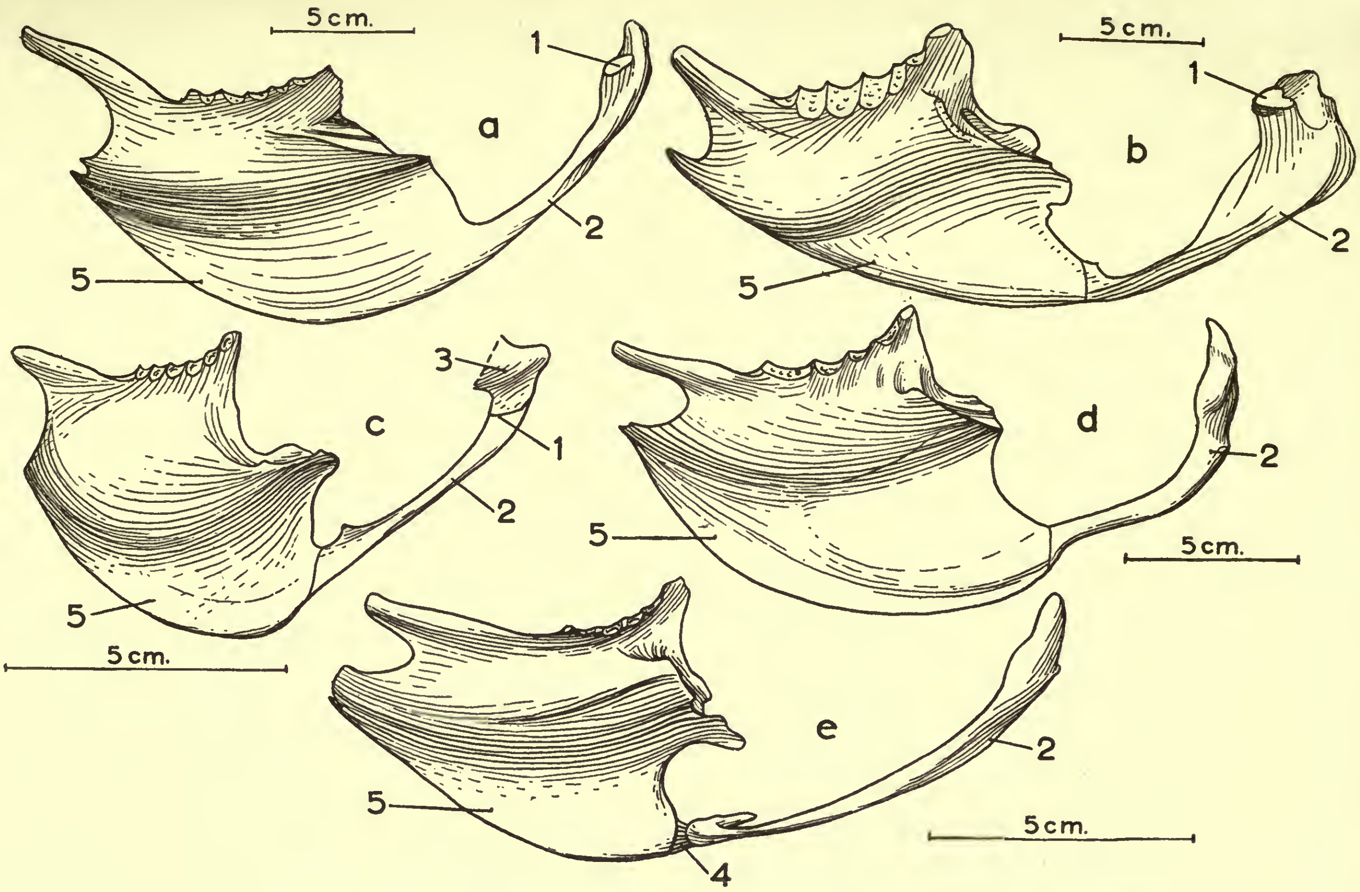
In the Ciconiidae, although the hypocleideum of the furculum joins the carina sterni, it forms a bony fusion with it only in some specimens of one genus, *Leptoptilos*, and the suture is always obvious. Unlike the Pelecani, each clavicle forms a sigmoid curve in lateral view. The dorsal part of the curve is convex anteriorly, and the ventral part, where the clavicles unite in the mid-line is concave anteriorly. There is no indication of an acrocoracoid flange in any of the Ciconiidae.

The furculum of the larger Ardeae is mainly like that of the Ciconiidae. The joint between the hypocleideum and the carina sterni is always ligamentous. The presence of a small interclavicle is characteristic of the Ardeae, and it is not found in the other groups considered here.

The hypocleideum of *Balaeniceps* is fused to the carina sterni as it is in *Fregata* and most adult specimens of *Pelecanus*. The suture is obliterated by ossification in all the British Museum specimens. The clavicle of *Balaeniceps* forms a continuous arc from the coracoid to the carina sterni, as it does in the Pelecani. This character may not be significant, as the clavicle of *Fregata* is in a slightly sigmoid curve and that of *Cochlearius* is almost in a continuous curve. The acrocoracoid flange is well developed in *Balaeniceps*, a character typical of the Pelecaniformes.

(2) *Sternum*

In *Balaeniceps* the sternal keel extends along the whole length of the sternum to the posterior border as it does in the Ciconiidae, Ardeae and most other birds. In *Pelecanus*, *Sula* and *Phalacrocorax* it only reaches half-way back from the anterior end of the sternum. Parker (1860 : 329) considered this a significant difference between *Balaeniceps* and the Pelecani, but apparently was not aware of the condition


5 cm.
a
1
2
5
5 cm.
b
1
2
5
c
3
1
2
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5 cm.
d
2
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5 cm.
e
2
5
4
5 cm.

FIG. 4. Diagrams of lateral views of sterna of (a) *Balaeniceps rex*, (b) *Pelecanus erythrorhynchuse*, (c) *Fregata ariel*, (d) *Ciconia ciconia*, (e) *Ardea goliath*.

1 = Acrocoracoid flange, 2 = clavicle, 3 = coracoid,
4 = ligament, 5 = sternum.

in *Fregata*, in which the keel extends almost to the posterior end of the sternum. Thus within the Pelecaniformes both types of keel occur.

C. *Pelvic Girdle*

Parker (1861 : 336) considered the pelvis of *Balaeniceps* to be " typically ardeine " because it was narrow like that of the Ardeae. Chalmers Mitchell (1913 : 696) thought it more like the ciconiid pelvis because it had a notch in the posterior border, like the Ciconiidae, and lacked the ridge on the ilium which is present in the Ardeae. However, the shape and details of the pelvis in birds seem to depend mainly on the function and relative size of the legs and leg muscles, and the pelvis is probably a very adaptable part of the skeleton. In the Pelecaniformes, for example, the pelvis of *Pelecanus*, a bird with strong legs, seems to have very little in common with that of *Phalacrocorax*, in which the legs are weaker and used mainly for swimming, or of *Fregata*, in which the legs are very weak and only used for perching. In groups in which there is less adaptive radiation, such as the Ciconiidae, or Ardeae, the function of the legs is more uniform and the shape of the pelvis varies little within the group, the main differences being in size. In *Balaeniceps* the pelvis is roughly the same shape as it is in the Ardeae and some Ciconiidae, but it differs from both in details. It seems even less like that of any of the Pelecaniformes, but as there is already a good deal of variation of the pelvis in this group *Balaeniceps* would perhaps be less out of place with them than with the Ciconiidae or Ardeae.

D. *Hind Limb*

(1) *Tibio-tarsus*

There are two forms of the distal condyles and the inter-condylar sulcus of the tibio-tarsus in the groups considered here. One is found in the Pelecani, Fregatae and Ardeae. In it the distal condyles are roughly semicircular in lateral view and the distal border of the outer condyle has no notch. The anterior aspect of the inter-condylar sulcus is fairly shallow, and the knob on the tarso-metatarsus which fits into it is not well developed. This type of articular surface is probably unspecialized, as it occurs throughout the Pelecani and Fregatae, in which there is considerable variation in the function of the legs, and in the Ardeae, in which the legs are long and unlike those of any of the pelican groups.

A second form occurs in the Ciconiidae. In it the distal borders of the condyles are flattened, and the condyles themselves are elongated posteriorly, so that they are oval in lateral view. There is a notch in the distal border of the outer condyle. The anterior aspect of the inter-condylar sulcus is deep, and proximal to it there is a hemispherical depression with a prominent knob immediately beside it. The knob on the tarso-metatarsus is much larger than in the first type, and articulates with the hemispherical depression when the leg is bent. The second condition apparently only occurs in long-legged birds, such as the Threskiornithidae and Phoenicopteridae, and to a lesser extent in the Gruidae and long-legged Charadrii.

The form in *Balaeniceps* is similar to that of the Pelecani, Fregatae and Ardeae.

(2) *Tarso-metatarsus*

In most groups of birds the hypotarsus is well ossified to form a varying number of " bridges " which enclose the flexor tendons in bony tubes. Of the Pelecani, *Phalacrocorax* has one tube and *Sula* and *Pelecanus* two.

In contrast, the Ciconiidae have a so-called " simple " hypotarsus. It consists of two parallel bony ridges with a groove between. The flexor tendons lie in this groove and are supported by unossified ligaments instead of bony bridges.

The Ardeae have a more ossified hypotarsus, rather like that of the Pelecani. In most genera there is only one tube, but the smaller genera sometimes have more.

Balaeniceps has two complete bony tubes through the hypotarsus. Their arrangement is strikingly like that of *Pelecanus*, and quite unlike the Ciconiidae.

(3) *First metatarsal*

In the Ciconiidae and Ardeae the first toe points backwards. In the Pelecani it is joined to the second toe by a web and is restricted to a lateral position, although it is mobile enough to be able to be pointed forwards. Parker (1861 : 344) says that in *Balaeniceps* the first toe is " very mobile " and is turned " very far inwards " when walking. Photographs show that it is directed backwards when the bird is standing still.

The position of the first toe influences the form of the first metatarsal. When the toe normally points backwards the metatarsal, if straight, would lie in the same plane as the flexor tendons of the other digits and interfere with their functioning. But the shape of the metatarsal is modified, usually giving it the appearance of bending round to one side of the tendons, and it often has a diagonal groove in which the tendons run freely.

In *Pelecanus*, in which the first toe does not point backwards, the metatarsal is straight, with only a shallow depression, mid-way along its length, where it touches the flexor tendons. In the other Pelecani this depression varies in size and depth, but it is never so marked as it is in the Ciconiidae and Ardeae. In *Sula* and *Phalacrocorax* the metatarsal is slightly bent round the flexor tendons.

In the Ciconiidae there is a broad, deep, diagonal trough for the flexor tendons, and the metatarsal appears twisted through an angle of about 90°. In the Ardeae the first metatarsal does not press against the flexor tendons as closely as it does in the Ciconiidae, because of the way in which it articulates with the first phalanx. As a result the diagonal groove in which the tendons lie is less marked than it is in the Ciconiidae and narrower than it is in the Pelecani.

In *Balaeniceps* the metatarsal has a depression for the flexor tendons which is very little deeper than that of *Pelecanus*. It is shallower than that of the Ciconiidae and broader than that of the Ardeae. The metatarsal appears slightly twisted, though less so than it is in the Ciconiidae. The form of the first metatarsal and the function of the first toe of *Balaeniceps* therefore seem to be more like those of the Pelecani than the Ciconiidae or Ardeae.

(4) *Toe articulations*

The proximal articulating surfaces of the basal phalanges of the second, third and fourth digits are fairly alike in the Pelecani and Ciconiidae, being roughly square in shape. In the Ardeae each of these articulating surfaces has a characteristic, irregular shape. *Balaeniceps* is like the first two groups, with the articulations almost square in proximal view.

SOME NON-SKELETAL PELECANIFORM CHARACTERS OF *BALAENICEPS*

(*a*) von Heuglin (1873 : 1095)

The egg is white with chalky lumps. Similar chalky lumps and nodules occur on eggs of *Phalacrocorax* and *Sula*.

Birds join up in parties to herd shoals of fish into corners. This communal fishing is characteristic of some *Phalacrocorax* and *Pelecanus* species.

(*b*) Chalmers Mitchell (1913)

The rhamphotheca is compound, as it is in the Pelecani and Fregatae.

A pyloric chamber is present in the stomach, as in *Pelecanus*.

The dermo-temporalis, biventer maxillae, temporal and pterygoid muscles are similar in *Pelecanus*.

There are no intrinsic muscles of the syrinx in *Balaeniceps* and *Pelecanus*.

The hyoid muscles are " excessively like those of *Pelecanus*."

The division of the pectoral muscle is similar in *Pelecanus*.

The arrangement of the wing tendons is the same in *Pelecanus*.

(*c*) Technau (1936 : 567)

The secondary nostrils can be closed, as in *Pelecanus*.

(*d*) Glenny (1955)

The right carotid is absent in *Balaeniceps* and some Pelecaniformes. When one carotid is missing in the Ciconiiformes it is the left one.

DISCUSSION

Those who have studied *Balaeniceps's* affinities from its skeleton seem to have been mainly concerned with its heron-like or stork-like features, and have neglected to consider its likeness to the pelicans. Jardine (1852) may have been responsible for this when he noted what he thought were significant differences from the " true pelicans ". Earlier impressions of *Balaeniceps* however were that it was near the pelicans. For example, its first mention in literature was by Ferdinand Werne (1848 : 143) who recorded that on 15th December 1840, " During my siesta someone saw a water bird that seemed to be as big as a young camel, which actually had a beak just like a pelican's, only without the pouch beneath it ". Even Gould (1852) referred to it as a kind of pelican, and Chalmers Mitchell (1913 : 701) considered that this opinion was " at least as happy as the more confident statements of later writers". None of the non-pelican characters given by Jardine are skeletal. No evidence from comparative osteology has been given as a reason for not putting *Balaeniceps* with the Pelecaniformes, although this has usually been implied on the few occasions when differences between *Balaeniceps* and the Pelecaniformes have been described. For example, Parker (1860 : 329) when describing the sternum, mentions that the keel extends to the posterior end of the sternum in *Balaeniceps*, as it does in the storks and herons, " whereas in the Pelicans, Gannets and Cormorants it scarcely continues beyond the middle of that bone ".

On the other hand, skeletal characters common to *Balaeniceps* and the Pelecaniformes have often been referred to. Sometimes they have been attributed to convergence (Parker 1861 : 308), or to the " common inheritance " of the Pelecaniformes and Ciconiiformes (Chalmers Mitchell 1913 : 699), but more often they are mentioned without comment or even without reference to the fact that they occur in both *Balaeniceps* and the Pelecaniformes. These characters are summarized below. They are arranged under three headings, and when a character is mentioned by more than one author, or under more than one heading, it is only referred to the first time it occurs on the list. Only original works are referred to. An asterisk is placed against the characters considered in the present investigation.

CHARACTERS OF BALAENICEPS'S *SKELETON THAT ALSO OCCUR IN THE PELECANIFORMES.*

A. *Noted and commented on by authors*

Parker (1861 : 308)

* The palatines have the " same essential structure " in other fish eating birds, such as the Pelican, Cormorant and Gannet, because the " motions of the upper jaw on the cranium " are the same.

Chalmers Mitchell (1913 : 699)

* Long lachrymals.
* Mesial ankylosis of the palatines.
Shell-like paroccipital processes.
* Clavicle ankylosed to carina sterni.
Shape of the head of the humerus.

He says these are either due to " convergent modifications between birds which, after all, are not very far apart in the system " or to the " common inheritance " of the Pelecaniformes and " their immediate allies ".

Böhm (1930 : 700)

Balaeniceps resembles *Pelecanus* in its closed palate.
* Hook to premaxilla.
* Bony nasal septum.
Complete interorbital septum.
Well developed postorbital process.
Lack of a postangular process on the lower jaw.

He says the Pelecaniformes are more like the herons than the storks, except for *Pelecanus* which is atypical, and more like the storks and *Balaeniceps*.

B. *Noted by authors, without comment*

Parker (1860)

Cervical vertebrae have haemal arches (p. 328).
* Furculum articulates with acrocoracoid flange (p. 329).
Tongue is small (p. 330).

Parker (1861)

" General class resemblance " in occipital region (p. 275).
Sudden bend in furculum (p. 340).

Chalmers Mitchell (1913)

* Nasal groove (p. 690).

C. *Mentioned by authors, without reference to the Pelecaniformes*

Parker (1861)

* Arrangement of the articulating surfaces of the quadrate and lower jaw (p. 310).
Ischium is longer than ilium posteriorly (p. 337).
No prepubic process (p. 337).
Wing skeleton—Parker says this is like that of the herons (p. 342) ; I found it as much like that of *Pelecanus* as *Ardea*.
Well developed " cnemial ridges " in tibio-tarsus (p. 343).
Slight sigmoid curve at distal end of tibio-tarsus (p. 343).
" Anterior cavity " at proximal end of tarso-metatarsus is deeper than in *Ardea* (p. 343).
* Complex hypotarsus (p. 344).
* Mobile hallux (p. 344).

Chalmers Mitchell (1913)

A rounded notch separates the metasternum from the posterior lateral processes of the sternum (p. 694).
Bases of coracoids do not meet in the mid-line (p. 696).
A notch separates the posterior ends of the ilium and ischium (p. 696).
No horizontal ridge formed by the " dorso-lateral edge of the post-acetabular ilium " (p. 696).
A tibial bridge is present (p. 697).

Of these skeletal characters common to *Balaeniceps* and the Pelecaniformes, some have been described as being due to " convergence " and others to " common inheritance ". It is one of the problems of taxonomy to distinguish between these two causes. In this instance the problem is to determine what are significant taxonomic characters in the pelecaniform skeleton. At the same time it might not be out of place to refer to the wider problem of the taxonomic significance of osteological characters One point of view is that bone is not an easily adapted substance, and that therefore phylogeny is readily determined from an examination of the skeleton. Verheyen (1953 : 480), for example, says that " systematics based on comparative osteology is perfectly realizable " since osteological characters are " practically invariable " and are " sheltered from the adaptations and modifications imposed by frequent habit ". There is clearly a good deal of truth in this, but it is a point of view that should be regarded with caution. There is evidence to show that bone is a plastic substance readily moulded by any change in the forces exerted by the muscles attached to it. This opinion is expressed, for example, by Weinmann & Sicher (1947 : 120) who say, " if it be true that functional stresses shape the bone, then it is equally true that a change of strength or direction of forces will lead to changes in the form and structure of bones ". Changes in muscle function related to changes in habit are therefore reflected in the skeleton. Similarities in habit of unrelated species and differences in habit of related species can produce a crop of adaptive osteological characters which may obscure phylogeny. Phylogeny may be apparent only in a number of small characters which have been relatively unaffected by adaptive changes. The sum of these characters may be peculiar to a particular group. Although the members of such a group vary in appearance and habit, and show convergence with other groups, they will have most of the small characters typical of their group. These " non-adaptive " characters differ from group to group and may occur in different parts of the skeleton, so that each group must be studied separately to get the " feel " of its typical characters.

In the light of these observations it will be understood that a " pelicaniform character " is hard to define precisely. The skeletal characters considered here are mainly those which distinguish the Pelecani and Fregatae from the Ciconiidae and Ardeae. Some of them, for example the acrocoracoid flange, also occur in other groups of birds. For this reason authors have not regarded it as important that *Balaeniceps* has them (Chalmers Mitchell, 1913 : 695). However, they have been included here because it is now understood that any given character may be taxonomically significant in one group, but not necessarily in another (e.g. see Cain, 1954 : 268). The acrocoracoid flange distinguishes the Pelecani, Fregatae and *Balaeniceps* from the Ciconiidae and Ardeae, but not from the Scopidae, Falconiformes, most Charadriiformes, Columbidae, Strigiformes, some Procellariiformes, and many other groups. It is not intended to imply that all the groups with an acrocoracoid flange are related, or that any of them are necessarily more closely related to the pelicans than to the storks.

Not all the " pelicaniform characters " considered here occur throughout the Pelecani and Fregatae. Sometimes one genus, or more, may differ in one feature from the others. For example, adults of *Anhinga* and *Sula* have no hook at the tip of the premaxilla, but they are typical in most other respects.

In other cases there may be a general trend, or tendency within the group, towards a certain condition, though all the genera are not necessarily concerned in it. One example of this is the tendency for reduction of the antorbital vacuity. In

Pelecanus, the antorbital vacuity is large, as it is in most birds ; in *Fregata*, *Phalacrocorax*, *Anhinga* and *Sula* it becomes progressively reduced. *Balaeniceps*, therefore, with no antorbital vacuity, would complete the series.

Sometimes an underlying pattern can be traced in a structure, with differences in details in each genus. A good example of this is the arrangement of the quadrate condyles in the jaw articulation (see Text-figures). The general form of the nasal cavity and of the palate possibly come into this category. In each of these instances *Balaeniceps* has the same underlying pattern as the Pelecaniformes, but the storks and herons do not.

To sum up, the general skeletal features which can be described as " pelecaniform " and which occur in *Balaeniceps* but not in the storks and herons are as follows :

(1) Position of nasal groove along upper mandible, and strong terminal hook (see A(1) and A(2)).
(2) Arrangment of nasal cavity (see A(3) and A(4)).
(3) Relationship of bones of palate and maxillopalatines (see A(5)).
(4) Size of lachrymal and antorbital vacuity (see A(6)).
(5) Type of jaw articulation (see A(7)).
(6) Some features of the pectoral girdle and sternum (see B).
(7) Shape of first metacarpal (see D(3)).

In my opinion the skeleton of *Balaeniceps* has many points of similarity, due to convergence, with the Ciconiidae and Ardeae, but, in spite of its difference in outward appearance from any of the Pelecaniforms, it shares several apparently non-adaptive features with them. I find it difficult to account for this unless *Balaeniceps* is more closely related to the Pelecaniformes than it is usually considered to be. Therefore, from a consideration of the skeletal characters of *Balaeniceps rex*, it seems that this species could occupy a monotypic family in the order Pelecaniformes, possibly near the Pelecanidae.

SUMMARY

1. A number of features of the skeleton of *Balaeniceps rex* were found to be more like the pelicans than either the storks or herons, with which *Balaeniceps* is usually grouped.

2. A study of the literature showed that the pelican-like characters of *Balaeniceps* had never been fully investigated.

3. The skeleton of *Balaeniceps* was compared with those of all the families of the Pelecaniformes, except the Phaëthontidae, and with the Ardeidae, Cochlearidae and Ciconiidae of the Ciconiiformes. Reasons are given for limiting comparison to these groups.

4. The characters common to *Balaeniceps* and the Pelecaniformes are described in detail.

5. The osteological evidence suggests that *Balaeniceps* is more closely related to the Pelecaniformes than to the Ciconiiformes, and the family Balaenicipitidae may reasonably be placed in the Pelecaniformes, possibly near the Pelecanidae.

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PLATE

[Scale : The skulls have been variously reduced, so that the crania are of approximately the same size. The actual total length of each skull is given below in brackets.]

Lateral views of skulls of :

(1) *Balaeniceps rex* (265 mm.).
(2) *Pelecanus onocrotalus* (410 mm.).
(3) *Sula bassanus* (180 mm.).
(4) *Ciconia ciconia* (255 mm.).
(5) *Ardea goliath* (235 mm.).
(6) *Cochlearius cochlearius* (125 mm.).

E = external naris.
G = nasal groove.
H = premaxillary hook.
I = position of internal nares.
L = lachrymal.
M = maxillopalatine.
P = palatine.
V = antorbital vacuity.

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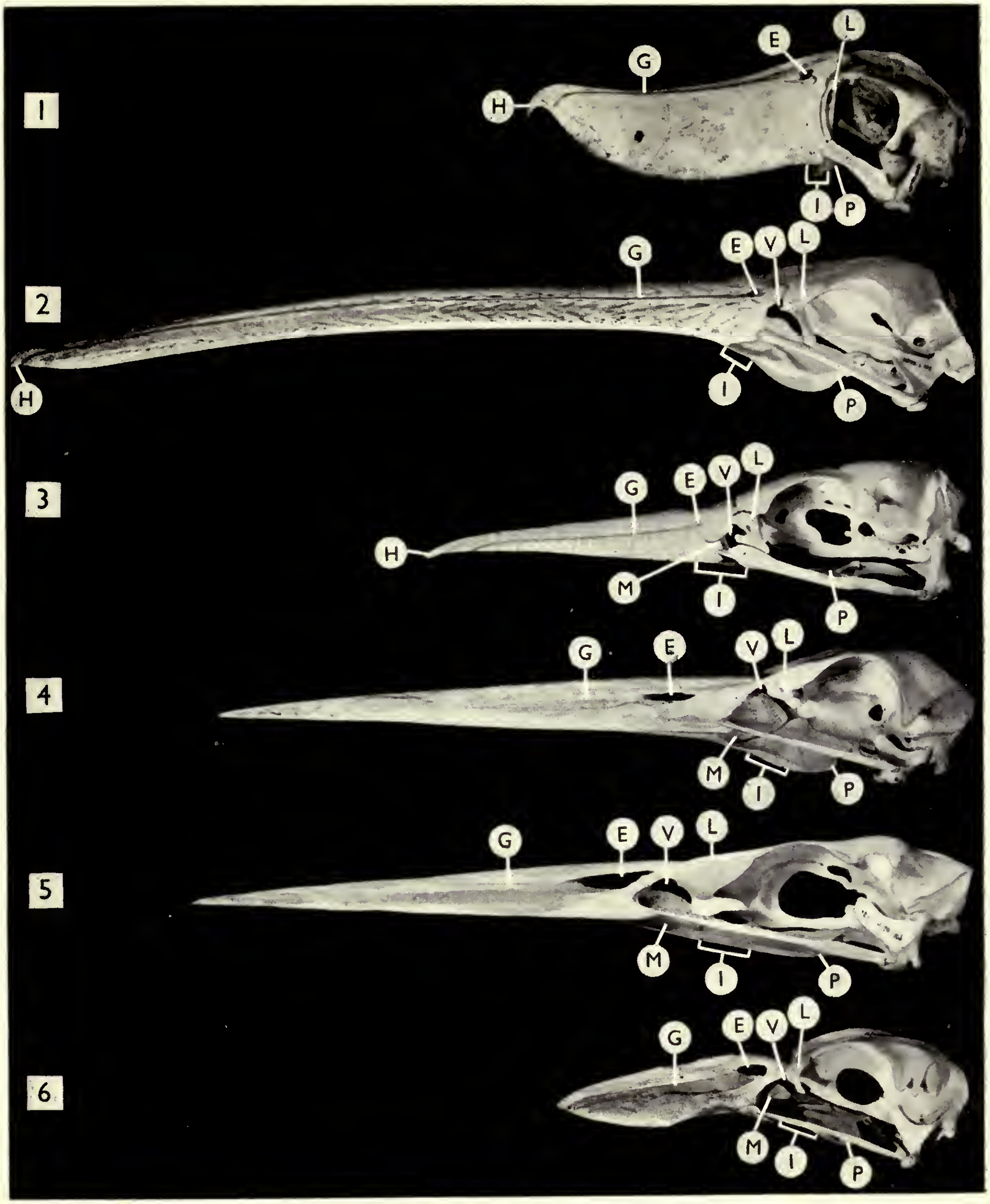
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NATURAL HISTORY

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PART II: *H. SAUVAGEI* (PFEFFER), *H. PRODROMUS* TREWAVAS, *H. GRANTI* BLGR., AND *H. XENOGNATHUS* SP. N.

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BY

P. H. GREENWOOD

East African Fisheries Research Organization, Jinja, Uganda.

Pp. 76–97 ; *Plate* 4 ; 8 *Text-figs.*

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PART II[1]: *H. SAUVAGEI* (PFEFFER), *H. PRODROMUS* TREWAVAS, *H. GRANTI* BLGR. AND *H. XENOGNATHUS*, SP. N.

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[1] Part I, see Greenwood, 1956*b*.

INTRODUCTION

MORPHOLOGICALLY, the *H. sauvagei* complex stands apart from any other species-group in Lake Victoria. The principal group character is that of the dentition which combines recurved outer teeth with multiseriate inner tooth-bands (Text-fig. 3).

Furthermore, the shape of the neurocranium, although differing intra-specifically within the group, is unlike that of other *Haplochromis*. This character is probably associated with the multiseriate dentition and relatively powerful jaw musculature. Indeed, amongst the non-piscivorous predators such marked divergence in cranial anatomy is otherwise only found in mollusc-eating species with hyper-developed pharyngeal bones and musculature. Two specifically constant forms of neurocranium occur in the " *sauvagei* " group, but neither can be correlated with the type of dental pattern present.

Trophically, members of the group may be classed as mollusc eaters, although available data indicate that other food organisms do contribute to their diet, usually in a subsidiary capacity. Unlike other mollusc-eating *Haplochromis* in this lake, species of the " *sauvagei* " group do not swallow the shells of their prey, but remove the soft parts before ingestion takes place. In this respect the feeding method is like that of *Macropleurodus bicolor* (Blgr.), a monotypic genus apparently derived from this group.

Haplochromis sauvagei (Pfeffer), 1896

(Text-fig. 1 and Pl. 1 upper fig.)

Ctenochromis sauvagei Pfeffer, 1896, *Thier. Afr. Fische*, 15.
Haplochromis nuchisquamulatus (part), Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 290.
Paratilapia granti (part), Boulenger, 1915, *op. cit.*, 342.
Paratilapia bicolor (part) Boulenger, 1915, *op. cit.*, 346.
Paratilapia retrodens (part), Boulenger, 1915, *op. cit.*, 235.
Haplochromis sauvagei (part), Regan, 1922, *Proc. zool. Soc., Lond.*, 167.
? *Paratilapia crassilabris* (part), Boulenger, 1915, *op. cit.*, 345.

I was unable to examine the holotype of *H. sauvagei* which was mislaid during the 1939–45 war ; at present the Berlin Museum authorities cannot confirm whether this specimen has been lost. Pending more definite information, no neotype can be selected, but, should such a step become necessary, I suggest that the specimen B.M. (N.H.) Reg. No. 1956.9.17.1, a male from Entebbe (Text-fig. 1) be given neotypical status.

Fortunately, Pfeffer's original description of *Ctenochromis sauvagei* is comprehensive, and, when coupled with a photograph of the type, clearly indicates to which *Haplochromis* species his specimen should be referred. The photograph, preserved in the British Museum (Natural History), is reproduced in Plate 1.

Additional material discloses only one important discrepancy with the original description, in which the mouth and lower-jaw profile are described as rising steeply : " . . . ; das untere Profil der Unterkinnlade steigt viel stärker. Die von dicken und breiten Lippen umgebene kurze Mundspalte steigt nach vom sehr steil auf."

In most specimens the ventral head profile is almost horizontal, or, at most, slightly oblique. A possible explanation for this discrepancy may lie in the fact that Pfeffer's description was taken from a fish preserved with its mouth open. From the photograph it is clear that, if the jaws were restored to their natural position, the cleft and lower jaw profile would be slightly oblique.

The present synonomy for *H. sauvagei* is essentially that prepared by Regan (1922), but some of the specimens which he referred to this species are now placed in others. In this connection, reference should be made to the list of study material.

Paratilapia crassilabris part (Boulenger, 1915) is tentatively retained in the synonomy on the basis of a single specimen (B.M. (N.H.) Reg. no. 1911.3.3.32). This individual cannot be identified with certainty, but it is nearer *H. sauvagei* than any other species with thickened lips and dentition not of the generalized type.

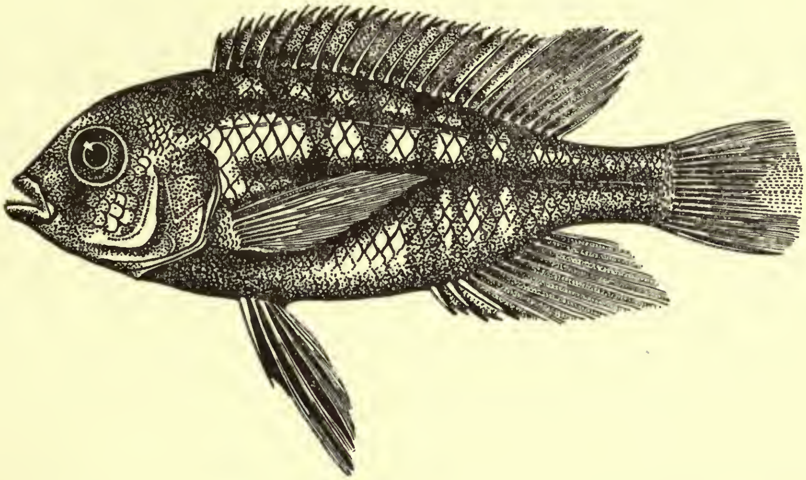

FIG. 1. *Haplochromis sauvagei*, ♂, B.M. (N.H.) 1956.9.17.1. Drawn by Miss L. Buswell.

Description. Based on 85 specimens, 58–105 mm. standard length. Of the measurements made, only cheek depth clearly shows allometry with standard length.

Depth of body 30·4–41·8, mean (M) = 35·6 ; length of head 29·6–34·5 (M = 31·9) per cent of standard length. Dorsal head profile varying from decurved to straight, but strongly sloping, the former shape occurring more frequently.

Preorbital depth 15·4–20·2 (M = 17·3) per cent of head length, least interorbital width 23·0–31·2 (M = 27·0) per cent. Snout as broad as long, its length 27·2–35·5 (M = 30·8) per cent of head ; eye diameter 25·7–33·4 (M = 28·9) per cent. Cheek becoming relatively deeper with increasing standard length ; four size-groups are recognized, 58–69 mm. S.L. (N = 13), 70–80 (N = 21), 81–90 (N = 27) and 91–105 (N = 24), for which the cheek depth is 21·0–25·0 (M = 23·2), 20·4–26·0 (M = 23·7), 22·0–26·9 (M = 24·4) and 24·1–26·6 (M = 25·1).

Caudal peduncle 13·9–19·3 (M = 16·4) per cent of standard length; its length 1·1–1·6, times its depth.

Mouth horizontal or slightly oblique; posterior maxillary tip reaching or almost reaching the vertical to the anterior orbital margin. Lips thickened; the depth of the upper lip, measured mid-laterally, is contained 4–4½ times in the eye-diameter. Jaws equal anteriorly, the lower 30·6–37·7 (M = 34·5) per cent of head length and 1·0–1·5 (mode 1·3) times as long as broad.

Gill rakers short, 7–9 (rarely 10) on the lower limb of the first arch.

Scales ctenoid; lateral line with 31 (f.7), 32 (f.29), 33 (f.39), 34 (f.9) or 35 (f.1) scales; cheek with 3–4 (rarely 2) series. 7–9 (less frequently 6) scales between dorsal fin origin and upper lateral line; 7 or 8 (less commonly 6 or 9) between pectoral and pelvic fin-bases.

Fins. Dorsal with 24 (f.11), 25 (f.56) or 26 (f.18) rays, anal 10 (f.1), 11 (f.10), 12 (f.71) or 13 (f.3), comprising XV–XVII, 8–10, and III, 7–10 spinous and branched rays for the fins respectively. Pectoral slightly shorter than the head, or occasionally of equal length. Pelvic with the first ray produced, variable in its posterior extension but longer in adult males than females. Caudal sub-truncate.

Lower pharyngeal bone triangular, its dentigerous area 1⅓–1¼ times as broad as long; pharyngeal teeth slender and cuspidate. In some specimens, teeth in the median rows are slightly enlarged, but retain their bicuspid crowns.

Teeth. In the outermost series of both jaws, the teeth have strongly recurved tips and are unequally bicuspid or unicuspid. The predominant tooth form is apparently correlated with length. Fishes less than 80 mm. S.L. have mainly bicuspid teeth, those in the range 80–90 mm. have either unicuspids or an admixture of uni- and bicuspids, whilst larger individuals possess mainly unicuspid teeth. When both types of teeth are present, the unicuspid form usually occurs anteriorly and laterally. There are 32–56 (mode 42) outer teeth in the upper jaw.

Inner teeth are either tri- or unicuspid; as in the outer series, unicuspid teeth are commoner in fishes above 80 mm. S.L. Antero-medially, the teeth are arranged in a broad band comprising 3–8 (mode 4) and 2–6 (modes 3 and 4) rows in the upper and lower jaws respectively. Laterally, the band narrows to a single series. A distinct inter-space separates the inner and outer series.

Syncranium and associated musculature. Neurocranial form in *H. sauvagei* departs quite considerably from the generalized *Haplochromis* type, and approaches that of *Macropleurodus bicolor* (Greenwood, 1956*a*). Essentially the same points of difference with the generalized type occur in both species. The skull has a foreshortened appearance due to the strongly decurved and almost vertically disposed ethmovomerine region. This curvature affects the morphology of the entire preorbital skull which is less gently curved than in the generalized neurocranium.

On the other hand, the jaws do not exhibit such radical departure from the generalized condition. The premaxilla, apart from a slight broadening of its dentigerous area, compares closely with that of other *Haplochromis*; the dentary is somewhat shorter, more massive and has a wider median dentigerous area than is common in generalized species. Consequent upon these modifications slight differences are apparent in the suspensorium.

Muscle disposition and form are similar to those of basic *Haplochromis* species. However, the *adductor mandibulae* I is slightly longer (38–44 per cent head length compared with 36–39 per cent) and broader (length/breadth ratio 3·0–3·7 cf. 4·4–5·5).

The syncranium, its musculature and the dentition all foreshadow the condition found in *H. prodromus*, and therefore that which reaches its ultimate expression in the genus *Macropleurodus* Regan (Greenwood, *op. cit.*). It is perhaps significant that variability in the degree to which the syncranium departs from the basic type is greater in *H. sauvagei* than in *H. prodromus*.

Causal factors responsible for the characteristic preorbital face in both *H. sauvagei* and *H. prodromus* are not readily determined. From an examination of larval fishes it is manifest that, as in *M. bicolor*, this form develops during post-larval ontogeny. It is probably effected by differential growth of various syncranial parts, especially since the ethmovomerine region is not directly affected by the moulding influence of muscle insertions. However, the premaxilla, which is closely associated both anatomically and functionally with the dentary, could exert considerable influence over this region. In *H. sauvagei* the dentary is short in relation to the head and also in comparison with other *Haplochromis* species of comparable size. If, during post-larval ontogeny, this bone increased in length more slowly than the neurocranium, and if it is to remain functionally integrated with the upper jaw, then there can be two morphological results : either a skull of the *H. sauvagei* type, or one in which the upper jaw projects anteriorly beyond the lower. A third possibility, that the suspensorium be rotated anteriorly, cannot be considered in this case, since its almost vertical alignment in *H. sauvagei* is typically that of the basic type.

H. sauvagei includes Gastropoda as a substantial part of its diet. As in *H.prodromus* and *M. bicolor* the soft parts alone are ingested. The feeding habits of *M. bicolor* have been described elsewhere (Greenwood *op. cit.*) : when feeding on snails, aquarium-kept *H. sauvagei* follow the same general pattern, except that after grasping the foot of the snail between its jaws the fish then uses the shell as a fulcrum to lever out the soft parts. Only rarely is the shell crushed by the jaws.

Coloration in life : Breeding males. Ground colour dark grey-green or blue-grey, lighter or yellowish ventrally ; a suffused coppery sheen on the flanks and ventral aspects of the operculum. Dorsal fin black basally, becoming slate-coloured distally ; lappets red ; red spots, often coalesced, between the soft rays. Anal dark with a red flush ; ocelli yellow. Caudal dark grey proximally, lighter distally, and with an overall orange-red flush. Pelvics black laterally, orange-red medially. *Non-breeding males* have similar coloration except that the copper flush is absent and other bright colours are less intense. *Females and immature males.* Ground colour golden-green, shading to pearly-white ventrally. All fins yellow-green.

In both sexes there may develop after death a dark longitudinal band running mid-laterally from the eye to the dorsal fin base, a second band running dorso-laterally approximately along the upper lateral-line, and 6–10 narrow transverse bars across the flanks. In life these markings are rarely discernible.

Amongst females a second type of coloration is known. This takes the form of irregular black blotches on a yellow ground and is identical with the *bicolor* pattern described for certain female *Macropleurodus bicolor*, *Hoplotilapia retrodens*, and *Haplochromis nigricans* (Greenwood, 1956*a* and *b*).

Since collectors show some predilection for fishes with a striking colour pattern, it is difficult to obtain accurate frequency estimates for the *bicolor* pattern. In the present sample, 25 per cent of females are *bicolor*. As most specimens were obtained by collectors aware of possible biasing factors, this figure may be accepted as fairly reliable. No male *bicolor* variants have yet been recorded. Thus, the incidence of *bicolor* variants seems sufficiently high to recognize the phenomenon as sex-limited polychromatism, and not merely the maintenance of an atypical genotype by recurrent mutation. Aberrantly coloured females were found in most localities. None exhibits a pattern intergrading with that usual for females.

Sex-limited polychromatism involving the same phenotypic expression was observed in *M. bicolor* and *Hoplotilapia retrodens* (Greenwood, 1956*a*). It seems probable that hypotheses regarding its genic basis and evolutionary significance in these species are also applicable to *H. sauvagei*. The possible significance of *bicolor* females as indicating phyletic relationship amongst the various species in which they occur has also been discussed (Greenwood, *op. cit.*). It was concluded that, in general, no reliability could be placed on this character, and that its repeated appearance was probably attributable to the oligophyletic origin of the Lake Victoria species-flock. Nevertheless, it is suggestive that both *H. sauvagei* and *M. bicolor* exhibit " *bicolor* " polychromatism as well as an apparent similarity in fundamental syncranial morphology.

Colour in preserved material : Adult males. Slate-grey to sooty, the longitudinal and transverse banding often obscured. Spinous dorsal fin grey, soft part hyaline but maculate. Anal and caudal hyaline. Pelvics black on the outer half, hyaline mesially. A dark lachrymal stripe and two bars across the snout are often present. *Females and immature males.* Ground colour variable, from silver-grey to brownish. Banding, as described above, usually developed. All fins hyaline, the soft dorsal and upper half of the caudal, maculate.

Distribution. Known only from Lake Victoria.

Ecology : Habitat. Restricted to littoral zones where the bottom is hard (sand or shingle) ; the species is especially common over exposed sandy beaches.

Food. The gut contents of forty-five fishes from various localities indicate that *H. sauvagei* feed mainly on Gastropoda (f.19), bottom deposits, which included insect larvae, Copepoda and diatoms (f.19), and Insecta (chiefly larval boring may-flies, *Povilla adusta* Navás) (f.4). No fragments of snail shell were observed, although opercula occurred frequently in the stomach and intestine (see also p. 79).

Breeding. Spawning sites and behaviour are unknown. In many localities, sexually active and quiescent fishes, and brooding females occur together.

The smallest adult fish was a female 72 mm. S.L. All specimens over 80 mm. were adult. No difference was detected in the sizes of adult males and females.

Diagnosis. H. sauvagei is distinguished from other *Haplochromis* in Lake Victoria by combinations of the following characters : lips thickened ; outer teeth with strongly recurved tips ; usually more than three inner rows of teeth in the upper jaw (mode 4). The species closely resembles *H. prodromus*, from which it may be separated by its slightly thinner lips and smaller adult size. In life, male breeding coloration serves to separate the two species.

Affinities. Similarity in the skull architecture and the dentition of *H. sauvagei* and *H. prodromus* suggest a phyletic relationship between the species. Consequent upon these anatomical similarities, the species show a close parallel in their feeding habits and food preferences, although in this respect *H. sauvagei* may be considered less specialized than *H. prodromus*.

Study material and distribution records

Museum and Reg. No.	Locality.	Collector.
	Uganda	
B.M. (N.H.) 1908.5.30.365–366 (as *Paratilapia granti*)	Bunjako	Degen.
B.M. (N.H.) 1906.5.30.371–372 (as *P. granti*)	Bugonga (Entebbe)	,,
B.M. (N.H.) 1906.5.30.413	Sesse Is.	Bayon.
,, ,, 1911.3.3.27	,,	,,
,, ,, 1909.3.29.9 (all as *P. bicolor*)	,,	,,
B.M. (N.H.) 1909.5.11.11	,,	,,
,, ,, 1906.5.30.374–377	Bunjako	Degen.
,, ,, 1956.9.17.1 (See Text-fig. 1)	Entebbe, Airport beach	E.A.F.R.O.
,, ,, 1956.10.9.1–25	,, ,, ,,	,,
,, ,, ,, ,, ,, 26–30	Entebbe, harbour	,,
,, ,, ,, ,, ,, 31–34	Bugungu (Napoleon Gulf)	,,
,, ,, ,, ,, ,, 35–36, 201	Jinja pier	,,
,, ,, ,, ,, ,, 37–40	Shore opposite Kirinya Point (Napoleon Gulf)	,,
,, ,, ,, ,, ,, 41	Kirinya Point	,,
,, ,, ,, ,, ,, 42	Old Bukakata	,,
,, ,, ,, ,, ,, 43	Katebo	,,
	Tanganyika Territory	
,, ,, ,, ,, ,, 44	Mwanza	,,
,, ,, ,, ,, ,, 45–72	Majita	,,
,, ,, ,, ,, ,, 73	Ukerewe Is.	,,
,, ,, ,, ,, ,, 74–75	Bukoba	,,
	Kenya	
,, ,, ,, ,, ,, 76	Kisumu	,,
,, ,, ,, ,, ,, 77–80	Kamaringa (Kavirondo Gulf)	,,
,, ,, ,, ,, ,, 81	Kach Bay (Kavirondo Gulf)	,,
,, ,, ,, ,, ,, 82	Open water 5 miles N. of Kendu (Kavirondo Gulf)	,,
,, ,, ,, ,, ,, 83	Rusinga Island	,,

Haplochromis prodromus Trewavas, 1935
(Text-figs. 2 and 3)

Paratilapia retrodens (part), Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 235.
Haplochromis ishmaeli (part), Boulenger, 1915, *op. cit.*, 293.
Haplochromis annectens Regan 1922 (nec. *Cyrtocara annectens* Regan, 1921), *Proc. zool. Soc. Lond.*, 167, fig. 2.

Description. Based on sixty-two specimens (including the holotype), 68–130 mm. S.L. None of the morphometric characters studied shows allometry with standard length.

In its general appearance *H. prodromus* closely resembles *H. sauvagei*, from which species it is distinguished by its thicker lips, slightly deeper cheek and larger adult size.

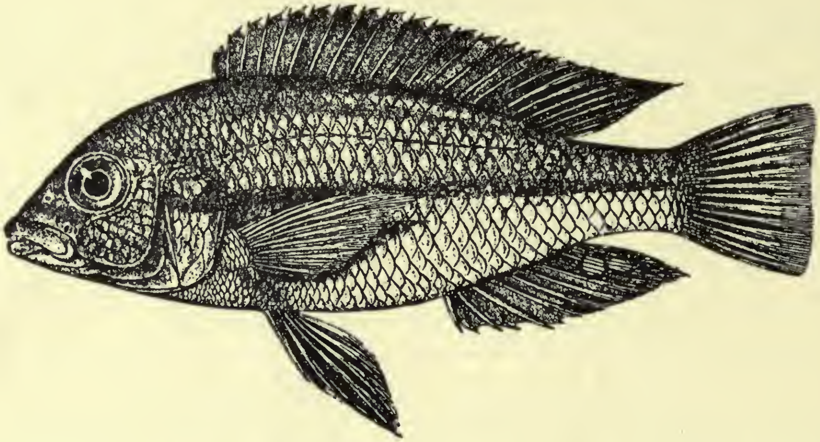

FIG. 2. *Haplochromis prodromus*, ♂, holotype (from Regan, the cichlid fishes of Lake Victoria, *Proc. Zool. Soc.*, 1922, 168, fig. 2).

Depth of body 32·8–40·0 (M = 36.2) ; length of head 29·4–33·6 (M = 31·5) per cent of standard length. Dorsal head profile somewhat variable, but always curved ; strongly decurved in some large individuals, less so in smaller fishes (70–75 mm. S.L.).

Preorbital depth 14·0–19·1 (M = 15·8) per cent head length ; least interorbital width 24·0–31·3 (M = 28·1) per cent. Snout as broad as or slightly broader than long, rarely longer than broad, its length 27·5–36·8 (M = 32·7) per cent of head ; eye diameter 25·8–33.3 (M = 27·8) ; cheek 22·0–30·5 (M = 26·7) per cent.

Caudal peduncle 12·6–18·1 per cent of standard length, its length 1·0–1·7 (mode 1·3) times its depth.

Mouth horizontal ; posterior maxillary tip reaching or almost reaching the vertical to the anterior orbital margin. Lips thickened ; the depth of the upper lip, measured mid-laterally, contained 3–3⅓ times in eye diameter. Jaws equal anteriorly, or infrequently the lower very slightly shorter ; lower jaw 30·5–37·8 (M = 34·3) per cent of head length, up to 1·3 (mode 1·1) times as long as broad.

Gill rakers short, 7–9 on the lower limb of the anterior arch.

Scales ctenoid; lateral line with 30 (f.1), 31 (f.7), 32 (f.16), 33 (f.35) or 34 (f.2) scales; cheek with 3 or 4 series. 7 or 8 (rarely 6½ or 9) scales between origin of dorsal fin and the lateral line, 7 or 8 (less frequently 9) between pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.7), 25 (f.40) or 26 (f.15) rays, anal with 11 (f.7), 12 (f.47) or 13 (f.8), comprising XV–XVII, 8–10 and III, 8–10 spinous and branched rays for the fins respectively. Pectoral shorter than the head. Pelvic fins with the first ray produced and of variable posterior extension, but reaching the anal fin in most adult fishes. Caudal sub-truncate.

Lower pharyngeal bone triangular, its dentigerous surface about 1½ times as broad as long; pharyngeal teeth slender and cuspidate; those of the median series sometimes enlarged.

Teeth. The dental pattern and tooth form in *H. prodromus* closely resemble those of *H. sauvagei.*

In the outer series of both jaws the teeth have strongly recurved tips and are unequally bicuspid or unicuspid. Bicuspid and weakly bicuspid teeth are the predominating forms in fishes less than 100 mm. S.L. Above this size most teeth are unicuspid. 26–56 (mode 40) outer teeth occur in the upper jaw.

Inner teeth are either tri- or unicuspid, the tricuspid form occurring most frequently in fishes less than 90 mm. S.L. Antero-medially the teeth are arranged in 3–7 (modes 4 and 5) and 3–6 (modes 3 and 4) series in the upper and lower jaws respectively. The posterior medial margin of the upper tooth-band is straight or slightly curved, that of the lower band is distinctly curved (Text-fig. 3).

The dental pattern of the holotype must be considered aberrant; it is not repeated in any of the sixty-one additional specimens. In the type, some posterolateral inner teeth are displaced medially from their series, thereby giving a spurious impression of a tooth band widened at that point. There is no increase in the width of the underlying premaxillary alveolar surface, nor is there an increase in the number of tooth rows (see fig. 14 in Regan, 1922). In all other respects the dentition of this specimen agrees closely with those described above.

Syncranium and associated musculature. The neurocranium and premaxilla of *H. prodromus* are virtually identical with those of *H. sauvagei.* The dentary, however, is relatively more massive and the mental profile is almost vertical.

Likewise, the jaw musculature compares closely with that of *H. sauvagei*, except that the *adductor mandibulae* I is somewhat shorter (36–39 per cent head length).

Observations made on the feeding methods of *H. prodromus* kept in aquaria, indicate that snails are removed from their shells in a manner similar to that employed by *Macropleurodus bicolor.* That is, the shell is crushed free by the jaws before ingestion takes place. The species was not seen to lever out the soft parts as is usual with *H. sauvagei.*

Coloration in life: Adult males. Ground colour slatey blue-grey; a peacock-blue sheen on the belly and ventral flanks. Chest and branchiostegal membrane black, operculum with a golden flush. Very faint indications of a dark mid-lateral stripe and seven transverse bars; also a faint lachrymal stripe. Dorsal dark, with a deep red flush between both spinous and soft rays; lappets orange. Anal sooty, ocelli deep yellow. Caudal sooty, with a faint orange flush along its posterior margin. Pelvics black. *Females and immature males.* Ground colour silver-grey above the mid-lateral stripe and silver below, with a faint peacock-blue flush on the flanks. Transverse barring is indistinct. Dorsal fin dark. Caudal and anal hyaline. Pelvics faintly yellow.

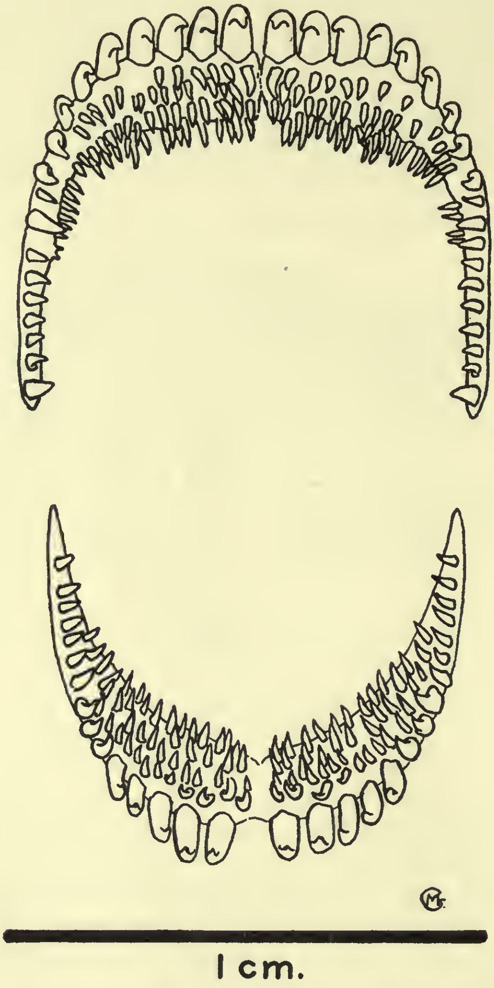

Fig. 3. The premaxillary and mandibular tooth bands in *H. prodromus.*

Colour in preserved material: Adult males. Ground colour dark grey; in some, faint traces of transverse and longitudinal banding. Chest and branchiostegal membrane black. Dorsal, caudal and anal dark, the soft dorsal maculate. Pelvics black. *Females and immature males.* Pale, banding variable but usually a distinct mid-lateral stripe and a faint, more dorsal band running along the upper lateral line; five to nine transverse bars across the flank. All fins hyaline.

Distribution. Known only from Lake Victoria.

Ecology: Habitat. Restricted to littoral zones, particularly where the substrate is hard (sand or shingle) and occurring less frequently over mud. Thus, the habitat of *H. prodromus* broadly overlaps that of *H. sauvagei*. Nevertheless, although biasing factors are introduced by the size selectivity of sampling gear and the limitations imposed by the habitat on the use of certain gear, it seems that *H. sauvagei* occur most frequently over shallow exposed beaches—where *H. prodromus* are less common—and that *H. prodromus* are more abundant in off-shore to deeper waters. This assumption is supported by results obtained when such non-selective collecting methods as explosives were used in both habitats.

Study material and distribution records

Museum and Reg. No.	Locality.	Collector.
	Uganda	
B.M. (N.H.) 1907.5.7.78 (holotype *H. prodromus*)	Buddu coast	Simon.
,, ,, 1906.5.30.379 (as *P. retrodens*)	Bunjako	Degen.
B.M. (N.H.) 1956.10.9 84–97	Jinja	E.A.F.R.O.
,, ,, ,, ,, ,, 98–99	Shore opposite Kirinya Point (Napoleon Gulf)	,,
,, ,, ,, ,, ,, 100–105	Beach near Nasu Point (Buvuma Channel)	,,
,, ,, ,, ,, ,, 106	Pilkington Bay	,,
,, ,, ,, ,, ,, 107	Hannington Bay	,,
,, ,, ,, ,, ,, 108–125	Entebbe harbour	,,
,, ,, ,, ,, ,, 126	Katebo	,,
,, ,, ,, ,, ,, 127–129	Busungwe Bay (Kagera river mouth)	,,
,, ,, ,, ,, ,, 130	Dagusi Island	,,
	Tanganyika Territory	
,, ,, ,, ,, ,, 131–133	Mwanza, Capri Bay	,,
,, ,, ,, ,, ,, 134–135	Godziba Island	,,
,, ,, ,, ,, ,, 197–199	Majita	,,
	Kenya	
,, ,, ,, ,, ,, 136–137, 196	Kamaringa (Kavirondo Gulf)	,,
,, ,, ,, ,, ,, 138	Kisumu	,,

Food. Stomach and intestinal contents of seventy-four fishes were examined. Of these, eleven were empty, fifty-seven contained only the remains of Gastropoda, three contained Gastropoda and Insecta, and three yielded unidentifiable sludge. Due to their very fragmentary nature the specific identification of molluscan remains was difficult; where identification was possible the genus *Bellamya* predominated. As many as twenty-two snail opercula were recorded from the intestine of a single fish, although the modal estimated number of snails per individual was about four.

Breeding. Sexually active and quiescent individuals were associated in all localities, but no data were collected on breeding sites or spawning behaviour. Only one female was found carrying larvae in the buccal cavity. There is apparently no sex-correlated adult size difference in this species ; the smallest sexually active individual was a male 102 mm. long.

Diagnosis. The same character complex serves to separate *H. sauvagei* and *H. prodromus* from the other *Haplochromis* of Lake Victoria. *H. prodromus* is distinguished from *H. sauvagei* by its larger adult size, thicker lips, slightly deeper cheek, and, in life, by male breeding coloration.

Affinities. The apparent phyletic relationship between *H. prodromus* and *H. sauvagei* on the one hand, and the more specialized *Macropleurodus bicolor* on the other, has been discussed above and elsewhere (Greenwood 1956*a*). In the latter paper, it was shown that Regan's suggested relationship between *H. prodromus* and *Platytaeniodus degeni* Blgr. can no longer be considered valid. Regan's views were based on the type and then unique specimen of *H. prodromus* whose dental pattern is aberrant. In any case, the posterior widening of the premaxillary dental surface is apparent and not actual in this fish, whereas in *P. degeni* the premaxilla undergoes a localized but distinct broadening during post-larval ontogeny.

Haplochromis granti Boulenger, 1906

(Text-figs. 4 and 5)

Paratilapia granti (part), Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 342, Fig. 231.
Haplochromis sauvagei (part), Regan, 1922, *Proc. zool. Soc., Lond.*, 167.

In Regan's revision of the Lake Victoria Cichlidae (*ibid.*, 1922), *H. granti* was treated as a synonym of *H. sauvagei*. After comparing the type with other specimens now available, I conclude that the two species should be regarded as distinct. This conclusion is supported by field observations. Both species have in common the " *sauvagei* " group characters of broad inner tooth bands, outer teeth with strongly recurved tips, and thickened lips. But they differ considerably in gross morphology and in certain details of dental pattern. The holotype of *H. granti* (figured in Boulenger, 1915) does not present a specifically typical appearance. However, its dental pattern indicates conspecificity with the specimens here described as *H. granti*. Furthermore, in the type, characters which contribute to gross morphology, for instance the form of the dentary and the head shape, intergrade with those of other specimens possessing a more typical facies.

One rather damaged specimen (B.M. (N.H.) Reg. No. 1911.3.3.28), identified by Boulenger as *Paratilapia retrodens* and later by Regan as *H. sauvagei*, should probably be referred to *H. granti*. Because of this uncertainty *P. retrodens* is not included in the revised synonomy of *H. granti*.

Description.—Based on the type, two paratypes and twenty-six additional specimens in the size range 70–122 mm. S.L. No clear-cut allometry with standard length was observed in the morphometric characters listed below.

Depth of body 32·7–39·3 (M = 35·4) ; length of head 28·8–33·3 (M = 31·5) per cent of standard length. Dorsal head profile slightly curved, or, less frequently, straight and gently to steeply sloping.

Preorbital depth 15·3–19·0 (13·3 in the smallest specimen) (M = 17·1) per cent of head length ; least interorbital width 25·0–32·8 (M = 28·6) per cent. Snout as broad as or slightly broader than long, its length 29·0–36·0 (M = 31·6) per cent of head ; eye diameter 25·0–31·0 (M = 27·5) ; depth of cheek 22·0–30·6 (M = 26·8) per cent.

Caudal peduncle 13·6–19·0 per cent of standard length, 1·2–1·7 times as long as deep.

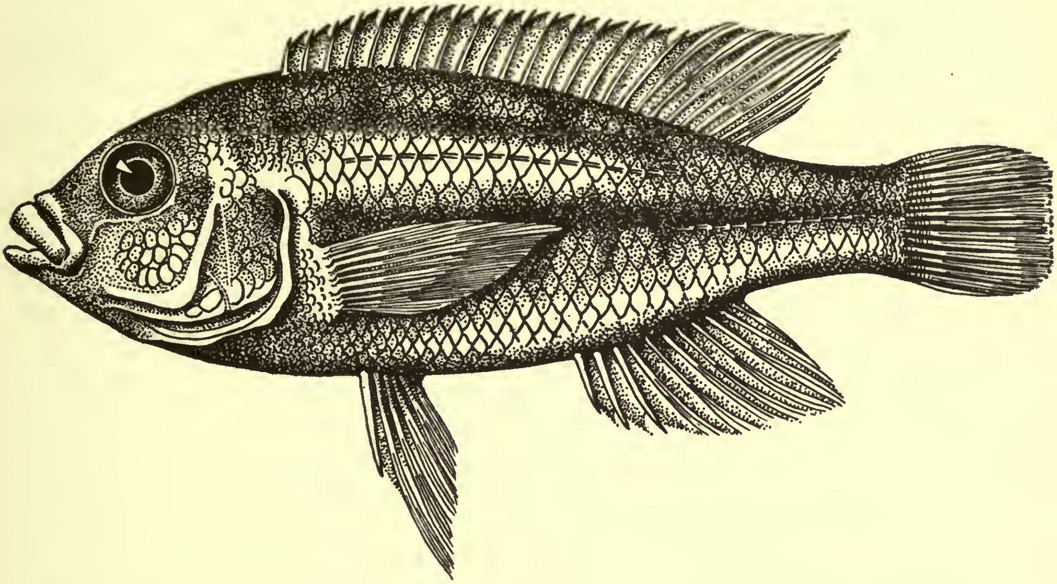

FIG. 4. *Haplochromis granti*, ♀, B.M. (N.H.) 1956.9.17.2. Drawn by Miss L. Buswell.

Mouth usually somewhat oblique ; posterior maxillary tip almost reaching the vertical to the anterior orbital margin, or occasionally reaching this line. Lips thick, sub-equally developed in a few specimens (e.g. the type), but the upper lip clearly thicker than the lower in most. Jaws equal anteriorly, or the lower jaw slightly projecting, its length 22·2–30·6 (M = 26·8) per cent of head length and 1·0–1·5 (mode 1·3) times its width.

The oblique mouth and unequally thickened lips give an appearance of deformity to many specimens. This impression is apparently misleading since there is no indication of any impairment to the efficiency of the jaw mechanism, either as a mechanical unit or in relation to feeding habits.

Gill-rakers short, 7–9 on the lower limb of the first arch.

Scales ctenoid, lateral line with 32 (f.9), 33 (f.11), or 34 (f.9) scales ; cheek with 3 or 4 (in one specimen 2) series ; 7 or 8 scales between origin of dorsal fin and lateral line ; 7 or 8 (rarely 9) between pectoral and pelvic fin bases.

Fins. Dorsal with 25 (f.11), 26 (f.17) or 27 (f.1) rays; anal 11 (f.7) or 12 (f.21), comprising XV–XVII, 9 or 10 and III, 8 or 9 spinous and branched rays for the fins respectively. In one specimen the anal fin had been damaged and subsequently healed irregularly, giving II, 10 rays. Pectoral shorter than the head, except in two specimens where it is of the same length. Pelvic fins extending to the vent in immature fishes and to the anal fin in adults; the first ray is proportionately more produced in sexually active males. Caudal fin truncate or sub-truncate.

Lower pharyngeal bone triangular, its dentigerous surface $1\frac{1}{3}$–$1\frac{1}{4}$ times as broad as long; pharyngeal teeth similar to those of *H. prodromus.*

Teeth. In the outer series of both jaws, the teeth are similar to those of *H. prodromus* and *H. sauvagei*; that is, unicuspid with strongly recurved tips. A few specimens—all below 90 mm. S.L.—have some bicuspid teeth situated postero-laterally in both jaws. There are 28–46 (mode, ill defined: 36) outer teeth in the upper jaw.

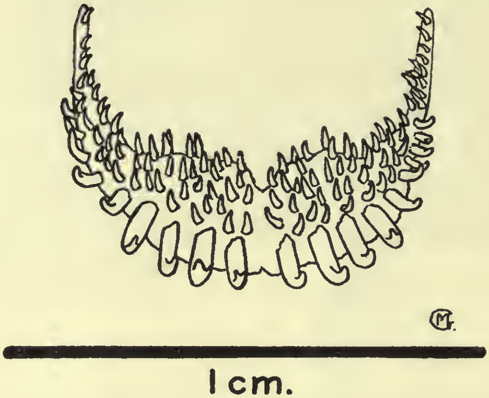

FIG. 5. Mandibular tooth band in *H. granti.*

The inner series are composed of tricuspid teeth in most fishes below 90 mm. and of unicuspid teeth in larger specimens. An admixture of both types is known from three fishes. The teeth are arranged in 2–6 (mode 4) rows in both jaws, but narrow to single series laterally. In many specimens the lower tooth band is wider than the upper; antero-medially, the posterior margin of this band is straight or very gently curved, thus contrasting with the lower series in *H. sauvagei* and *H. prodromus,* where the margin is clearly curved (Text-fig. 5).

Syncranium and associated musculature. The preorbital face of the neurocranium is intermediate in form between that of *H. sauvagei* and the generalized *Haplochromis* type. Greatest departure from the condition observed in *H. sauvagei* and *H. prodromus* is seen in the maxilla, which in *H. granti* is shorter and more bowed in its long axis. Also, the inner face of the posterior limb is markedly concave, which results in the outer face appearing more bullate than in other members of the "*sauvagei*" group. The dentary resembles that of *H. sauvagei* but differs in its less rounded, more angular, anterior outline.

Shortage of material allowed only two dissections of head musculature to be made. The major muscles are distributed as in *H. prodromus* and *H. sauvagei* but the origin of the *adductor mandibulae* I is deeper and more fan-shaped in *H. granti*. In the two specimens dissected, the length of this muscle (42 and 43 per cent of head) is somewhat greater than in *H. prodromus* but equal to that in *H. sauvagei*.

Coloration in life : Adult males. Ground colour light blue-grey ; branchiostegal membrane dusky, especially between the rami of the lower jaw. Dorsal fin blue-grey, darkest on the proximal third ; lappets orange-red, as are the spots and streaks between the soft rays. Caudal blue-grey, darker on the proximal half ; margin outlined in red ; orange-red spots between the rays. Anal dusky blue-grey, with an overall pink flush ; ocelli yellow. Pelvics black, faint pink mesially. *Females and immature males.* Coloration in life unknown.

Colour in preserved material : Adult males. Ground colour grey or brown ; branchiostegal membrane dark grey. An intense black mid-lateral stripe and often traces of a lachrymal stripe and 5–7 vertical bars across the flanks. Dorsal, caudal and anal fins hyaline or dusky ; pelvics black. *Females and immature males.* Ground colour silver-white, darkest dorsally. An intense mid-lateral stripe and often faint indications of an interrupted upper band running between the dorsal fin base and the upper lateral line. Seven to nine faint transverse bars are usually present on the flanks and caudal peduncle ; no lachrymal stripe. All fins hyaline.

Distribution. Confined to Lake Victoria.

Ecology : Habitat. Too few records are available to permit generalization on the habitat preferences of *H. granti*. The twenty-six specimens whose habitat had been recorded were caught in littoral zones and in water less than forty feet deep. Most localities represented in the collection can be classified either as sandy beaches on exposed shores or as exposed coastlines with a hard substrate. The few remaining localities are sheltered bays where the bottom is composed of organic mud.

Food. Twelve of the twenty-six fishes examined contained ingested material in the stomach or intestine. In each case only the soft parts of Gastropoda were found, except for some Lamellibranchiata shell fragments in one individual. From these admittedly few observations it is inferred that *H. granti* feed in a manner similar to that observed for *H. prodromus* and *H. sauvagei*.

Breeding. There is no information on any aspect of the breeding behaviour in this species ; all specimens below 90 mm. S.L. were immature.

Diagnosis. Haplochromis granti differs from other Lake Victoria *Haplochromis* in possessing broad bands of inner teeth (2–6, mode 4, series) in both jaws and by its unequally thickened lips, the upper usually thicker than the lower. This latter character, together with the oblique mouth and straight posterior margin to the inner tooth band of the lower jaw, serves to distinguish *H. granti* from *H. prodromus* and *H. sauvagei*.

Affinities. By virtue of its dentition, *H. granti* must be included in the *H. sauvagei*-*H. prodromus* species-group. Other characters probably associated with dentition, such as the shape of the premaxilla and dentary, are closely similar in all three species. But, despite resemblances in these dental and osteological characters, and in the associated musculature, the neurocranial morphology of *H. granti* has not departed so radically from the generalized *Haplochromis* type. Morphologically speaking, the relationship between *H. sauvagei* and *H. prodromus* is directly linear, whilst that of *H. granti* is somewhat divergent but with a parallel trophic trend.

Study material and distribution records

Museum and Reg. No.	Locality.	Collector.
	Uganda	
B.M. (N.H.) 1903.5.30.367 (holotype *P. granti*)	Bunjako	Degen.
B.M. (N.H.) 1903.5.30.368–369 (paratypes P. *granti*)	,,	,,
B.M. (N.H.) 1956.10.9.139	Bay opposite Kirinya Point (Napoleon Gulf)	E.A.F.R.O.
,, ,, ,, ,, ,, 140–141	Bugungu (Napoleon Gulf)	,,
,, ,, ,, ,, ,, 142–144	Beach nr. Nasu Point (Buvuma Channel)	,,
E. African Fisheries Res. Lab. Jinja	Pilkington Bay	,,
B.M.(N.H.) 1956.10.9.145–147	Thruston Bay	,,
,, ,, 1956.9.17.2	Ekunu Bay	,,
,, ,, 1956.10.9.148–152	Entebbe, harbour	,,
,, ,, ,, ,, ,, 153	Near Busungwe Is.	,,
,, ,, ,, ,, ,, 154	Busungwe Bay (Kagera river mouth)	,,
,, ,, ,, ,, ,, 155–157	Beach near Grant Bay	,,
,, ,, ,, ,, ,, 200	Buka Bay	,,
	Kenya	
,, ,, ,, ,, ,, 158	Kisumu	,,
	Tanganyika	
,, ,, ,, ,, ,, 159	Ukerewe Is.	,,
,, ,, ,, ,, ,, 160–163	Majita	,,

Haplochromis xenognathus sp. nov.

(Text-figs. 6 and 7)

The high intra-specific variability of *H. xenognathus* makes this species of particular interest when considering the evolution of monotypic cichlid genera. Some of the more aberrant specimens, if studied in isolation, might well be given a status equal with the monotypic genera recognized at present. Less extreme individuals, on the other hand are not immediately distinguishable from *H. sauvagei*.

The modal type tooth-pattern and the usual arrangement of the jaws are, however, unlike those of other species in the " *sauvagei* " group (Text fig. 7). I am led to include *H. xenognathus* in this group because of its " *sauvagei* "-like tooth form and the multiseriate dental pattern.

The sample provides sufficient intra-specific variation to indicate morphological stages through which the typical specific facies may have passed in its evolution from a form similar to the extant *H. sauvagei.*

Type specimen. A male, 91 + 19 mm. ; from Entebbe harbour.

Description. Based on thirty-five specimens 80–113 mm. S.L.

Depth of body 31·2–38·0 (M = 34·8) ; length of head 29·2–35·4 (M = 33·1) per cent of standard length. Dorsal head profile usually straight and somewhat steeply sloping ; curved in a few specimens.

Preorbital depth 16·0–20·7 (M = 17·7) per cent head length ; least interorbital width 23·5–29·0 (M = 26·8) per cent. Snout from $1\frac{1}{5}$–$1\frac{1}{3}$ longer than broad, its length 31·8–37·8 (M = 35.2) per cent of head ; eye 23·2–28·7 (M = 26·0) ; depth of cheek 23·2–28·7 (M = 26·0) per cent.

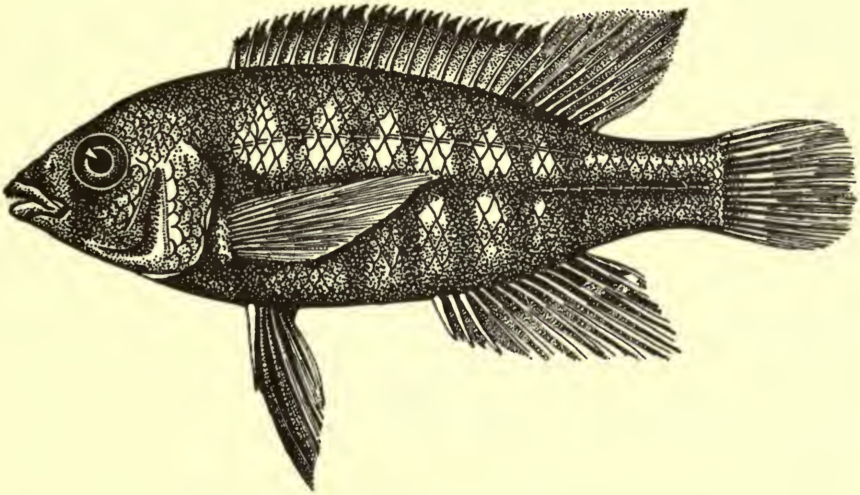

FIG. 6. *Haplochromis xenognathus*, ♂, holotype, B.M. (N.H.) 1956.9.17.3. Drawn by Miss L. Buswell.

Caudal peduncle 13·8–19·0 (M = 15·9) per cent of standard length ; 1·1–1·7 (mode 1·4) times as long as deep.

Mouth horizontal, the posterior maxillary tip reaching, or almost reaching, the vertical to the anterior orbital margin ; lips slightly thickened. The lower jar is clearly shorter than the upper in 74 per cent of the specimens examined and subequal to the upper in 26 per cent. Even in this latter group the outermost teeth of the lower jaw occlude behind the equivalent upper jaw series. Lower jaw 32·0–38·0 (M = 34·5) per cent of head, and 1·1–1·8 (mode 1·4) times as long as broad.

Gill rakers short, 7–9 (rarely 10) on the lower limb of the first arch.

Scales ctenoid ; lateral line with 31 (f.4), 32 (f.14), 33 (f.11), 34 (f.4) or 35 (f.2) scales ; cheek with 3 or 4 (rarely 2 or 5) series ; 6 or 7 (less frequently 8) scales between origin of dorsal fin and lateral line ; 7 or 8 (rarely 6 or 9) between pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.13), 25 (f.19), or 26 (f.3) rays ; anal with 11 (f.9), 12 (f.24) or 13 (f.1). One specimen has only two spines, giving a total count of 10 rays. The spinous and branched ray counts for the fins are XV–XVII, 8–10 and III, 8–10. Pectoral fins shorter than the head. Pelvic fins with first ray produced, extending to the anterior part of the anal fin in females and more posteriorly in adult males. Caudal truncate.

Lower pharyngeal bone triangular, its dentigerous surface $1\frac{1}{3}$–$1\frac{1}{4}$ times as broad as long. The pharyngeal teeth are slender and bicuspid, those of the median series not noticeably enlarged. In one specimen, the lower pharyngeal bone is stout, the toothed surface slightly longer than broad and the median teeth enlarged and molariform ; this fish also shows a somewhat atypical oral dentition, in that the teeth are bluntly cuspidate.

Teeth. Except in the smallest specimen, unicuspid teeth predominate in the outer series, but some weakly bicuspid teeth do occur postero-laterally in both jaws of large fishes. In the smallest specimen, the entire outermost series is composed of bicuspid teeth.

The outer teeth, like those of *H. sauvagei* and other species of the group, are relatively stout and have strongly recurved tips. In the lower jaw, the anterior teeth are implanted at an acute angle, so that their necks lie almost horizontally ; but recurvature of the crown is such that the tip points almost vertically upwards (Text-fig. 8). There are from 32–52 (mode 44) outer teeth in the upper jaw.

Teeth forming the inner series are small and either unicuspid or weakly tricuspid. Considerable variation exists in the number of inner rows. In general, teeth are disposed in a broad crescent which narrows abruptly at a point almost mid-way along the premaxillary limb. Thereafter, there is a single inner row. The antero-medial depth of this band varies with the number of tooth rows, of which there are from 3–9 in both jaws (modes 7 and 5 for the upper and lower jaws respectively). In fishes with markedly disparate jaws, the most posterior inner teeth of the dentary do not occlude with the upper series.

The toothed surface of the dentary is often slightly convex, so that when viewed laterally several points on the inner band are higher than the crowns of the outer teeth (Text-fig. 8).

Fishes with narrow tooth bands in both jaws have a dental pattern closely resembling that of *H. sauvagei* ; the resemblance to this species is enhanced by the sub-equal jaws of these specimens. In contradistinction, other *H. xenognathus* with sub-equal jaws have a broad and specifically typical tooth pattern.

Syncranium and associated musculature. The neurocranium of *H. xenognathus* is identical with that of *H. granti.* The shape of the premaxilla varies slightly in relation to the number of inner rooth rows, but is otherwise comparable with the premaxilla of *H. sauvagei.* Likewise the dentary is similar in the two species, except that the dentigerous surface is inclined forwards and downwards in *H. xenognathus.* Perhaps the most characteristic appearance of this bone is imparted by the almost horizontally implanted anterior teeth.

A syncranial skeleton prepared from a specimen with *H. sauvagei*-like facies did

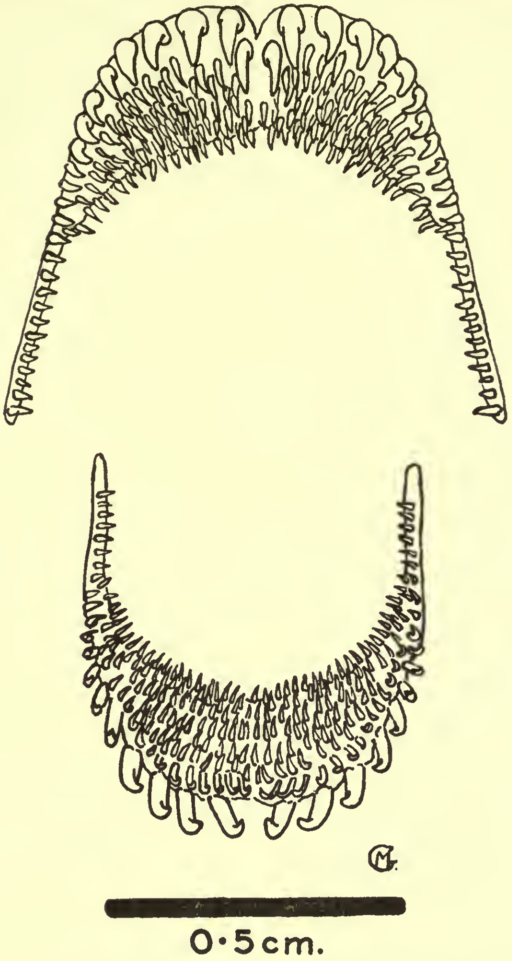

Fig. 7. Premaxillary and mandibular tooth bands in *H. xenognathus*.

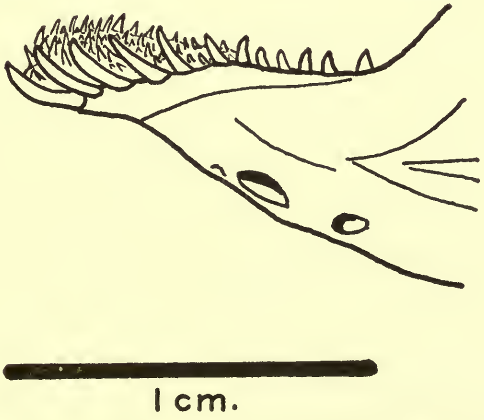

Fig. 8. Lateral view of the anterior part of the dentary of *H. xenognathus*.

not differ, beyond the limits of individual variability, from that of a typical specimen and was clearly distinguishable from that of *H. sauvagei*.

Head musculature in *H. xenognathus* is similar to that of *H. sauvagei* and *H. prodromus*. The *adductor mandibulae* I is shorter than in the former species, but is equal to that of the latter (33·2–39·4 per cent of head).

Coloration in life: Adult males. Ground colour dark bronze dorsally, shading to grey-bronze ventrally: cheek and operculum with a distinct bronze sheen; chest and branchiostegal membrane bluish-grey. Dorsal fin sooty, with red streaks between the soft rays; lappets red. Caudal dark, upper half with red spots, lower half flushed with red. Anal clouded; ocelli yellow. Ventrals sooty, the first ray bluish-white. Live coloration of *immature males* is unknown. *Females.* Ground colour as in males, but the branchiostegal membrane greyish. Dorsal fin with red lappets but lacking the red streaks. Caudal dark yellow ventrally, lighter and maculate above. Anal and ventral fins dark olive-yellow, the first pelvic ray bluish-white.

Colour in preserved material: Breeding males. Dark grey, the flank with a faint coppery sheen; a distinct lachrymal stripe. In some specimens five transverse bars may be discerned on the flanks. Dorsal, caudal and anal fins grey, the upper third of the caudal maculate. Pelvic fins black. *Non-breeding and immature males.* Ground colour silver-grey; 7–9 distinct transverse bars. Fins as above. *Females.* As for non-breeding males, except that the pelvics are colourless. In some specimens there is a fairly distinct mid-lateral stripe.

Distribution. Known only from Lake Victoria.

Ecology: Habitat. The few and scattered records indicate that *H. xenognathus* is confined to littoral zones where the substrate is hard. Most specimens in the collection were obtained from seine nets operated over exposed sandy beaches.

Food. Seventeen of twenty-three fishes examined contained ingested material in the stomach or intestine: in ten, only the soft parts of Gastropoda were found; in three, Insecta (chironomid and ephemerid larvae); in two, bottom detritus (sand-grains and plant tissue); and in three, unidentifiable sludge.

Although no observations have been made on living fishes, the presence of gastropod remains without shells suggests that the feeding methods of *H. xenognathus* are like those of *H. sauvagei*, *H. prodromus* and *H. granti*.

Breeding. No information is available. The smallest sexually mature fish was a female 87 mm. S.L.

Diagnosis. Haplochromis xenognathus may be distinguished from other species of the genus by the following characters: outer teeth with strongly recurved tips, those of the lower jaw implanted horizontally or almost so; inner teeth in the upper jaw arranged in a broad, crescentic band (3–7, mode 5 series); lower jaw usually much shorter than the upper and also with broad bands of teeth (3–9, mode 5, inner series). Some individuals closely resemble *H. sauvagei* both in gross morphology and in details of dentition, but may be distinguished by the peculiar implantation of their anterior lower teeth and by having a slightly narrower and longer snout; in life the coloration of both sexes is diagnostic.

Affinities. In many respects the species has departed considerably from the basic "*sauvagei*" type as represented by the nominate species. Yet, it is apparently with *H. sauvagei* that *H. xenognathus* shows greatest morphological affinity. The resemblance is most clearly seen in the least typical members of *H. xenognathus*, but is obscured in other forms. These latter individuals seem to indicate that if future evolution in *H. xenognathus* is continued along such lines and is coupled with a reduction in morphological variation, then the species could acquire a status equivalent to the monotypic genera recognized at present.

Study material and distribution records

Museum and Reg. No.	Locality.	Collector.
B.M. (N.H.) 1956.10.9.164–167	Jinja	E.A.F.R.O.
,, ,, ,, ,, ,, 168	Bay opposite Kirinya Point (Napoleon Gulf)	,,
,, ,, ,, ,, ,, 169	Beach nr. Nasu Point (Buvuma Channel)	,,
,, ,, ,, ,, ,, 170	Hannington Bay	,,
,, ,, 1956.9.17.3 (type)	Entebbe, harbour	,,
,, ,, 1956.10.9.171–173	,, ,,	,,
,, ,, ,, ,, ,, 174	Entebbe, Airport beach	,,
,, ,, ,, ,, ,, 175	Bugonga, Entebbe peninsula	,,
,, ,, ,, ,, ,, 176–177	Katebo	,,
,, ,, ,, ,, ,, 178–182	Beach south of Busungwe (Kagera river mouth)	,,
	Tanganyika	
,, ,, ,, ,, ,, 183	Bukoba	,,
,, ,, ,, ,, ,, 184–191	Majita	,,
,, ,, ,, ,, ,, 192–195	Mwanza, Capri Bay	,,

DISCUSSION

In an adaptively multi-radiate species-flock, the differentiation of true phyletic relationship from parallel trends is difficult, particularly when the flock, like that of Lake Victoria, is oligophyletic in origin. It has been noticed, however, that in many adaptive sub-groups some species show greater morphological affinity with one another than with other members. This I interpret as indicating that both lineal descent and parallel evolution have contributed to the origins of the groups.

The remarkable uniformity of the distinctively shaped outer teeth in all four members of the "*sauvagei*" complex probably indicates a monophyletic origin for the group. Their multiseriate dentition, on the other hand, cannot be considered of value in indicating phylogeny. Broad tooth-bands have evolved in several other and unrelated species, for example, the algal-grazers *H. nigricans* and *H. nuchisquamulatus*, and in certain monotypic genera.

As an ecologically defined group, the "*sauvagei*" complex exhibits considerable variation in species morphology. There are three distinctive forms, represented by

H. sauvagei and *H. prodromus*, *H. granti*, and *H. xenognathus*. The two first-mentioned species must be considered nearer the generalized type and the two latter as showing progressive but independent divergence.

When discussing the evolution of *Macropleurodus bicolor*, I drew attention to the possible relationship between this species and *Haplochromis prodromus* (Greenwood, 1956*a*). No conclusion can be reached at present, but the prospective adaptational significance of a " *prodromus* " type cranial anatomy in the evolution of *M. bicolor* cannot be disregarded. That both species should have almost identical feeding habits would seem to lend additional weight to this argument.

Morphological and ecological differences between *H. prodromus* and *H. sauvagei* are of the slightest order. If their lineal relationship can be accepted, one is tempted to consider the species in an ancestor-descendant category. In all probability, present-day *H. sauvagei* differ genotypically and even phenotypically from the presumed ancestral type, yet, despite these limitations, it is difficult to imagine a species more similar to *H. prodromus*. Several other such *Haplochromis* species-pairs are known from Lake Victoria. Each, except for their temporal coexistence, would fulfil the palaeontological requirements for ancester-descendant relationship. Indeed, co-existence, even within one habitat, of species which could be lineally derived appears to be a major feature of the Lake Victoria *Haplochromis* species-flock. The Lake's geological history provides a possible explanation of this phenomenon (Brooks, 1950 ; Greenwood, 1951). During the inter-Pluvial periods of the Pleistocene, Lake Victoria was probably reduced to a series of small lakes and swamps. Under such conditions a species would be isolated into several discontinuous groups. If some surviving populations underwent genic reorganization as a result of isolation, or of increased selection pressure, it is possible that they might retain their discreteness if brought into contact with the parental stocks when the lakes were joined during the succeeding Pluvial period. That the derived and parental species were able to coexist even when their ecological requirements were similar, seems to indicate drastically reduced selection pressure.

The third member of the " *sauvagei* " group, *H. granti*, is unlike either *H. sauvagei* or *H. prodromus*. However, the differences lie in characters which could be derived by heterogonic growth of certain cranial parts from a species less differentiated than *H. sauvagei*, but possessing the group dental characters.

From an evolutionary viewpoint, *H. xenognathus* is undoubtedly the most interesting species. When the first few specimens came to my notice, I considered them to be members of a distinct and apparently monotypic genus. The degree of morphological differentiation of this supposedly new genus was at least equal to that of *Hoplotilapia retrodens* Hilg. When more specimens were collected, however, it was obvious that the species was extremely variable and should be retained within the genus *Haplochromis*. The less typical specimens differed only slightly from *H. sauvagei*, whilst the typical fishes were clearly distinct from that species. Thus, it seems legitimate to look upon *H. xenognathus* as an example of a stage through which species might pass in the evolution of a genus.

Ecologically, the " *sauvagei* " group has entered an adaptive zone unique for *Haplochromis*, but occupied by two monotypic genera, *Macropleurodus bicolor* and

Hoplotilapia retrodens. All other known predominantly mollusc-eating *Haplochromis* species crush their prey by means of hypertrophied pharyngeal bones and dentition.

If, in conclusion, one considers the morphological and consequent ecological adaptations of the *H. sauvagei* group, the impression is gained of a species-complex partially advanced on the path of trophic specialization. From its present peak it could supply, and may even have supplied, raw material for further specialization.

SUMMARY

1. *Haplochromis sauvagei* (Pfeffer) 1896, and *H. prodromus* Trewavas 1935, are re-described.
2. The species *H. granti* Blgr. 1906, previously synonymized with *H. sauvagei,* is reinstated.
3. A new species, *Haplochromis xenognathus,* is described.
4. Data are given on the ecology of all four species.
5. Sex-limited polychromatism, involving a piebald female coloration, is described for *H. sauvagei.*
6. The evolutionary status of the species is discussed.

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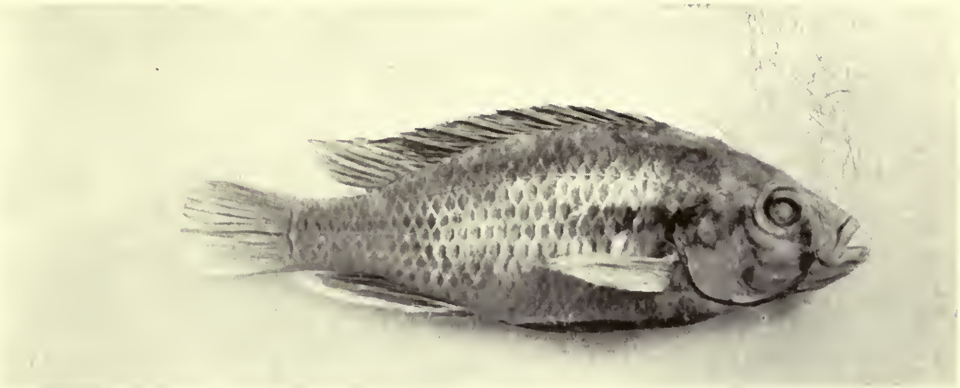
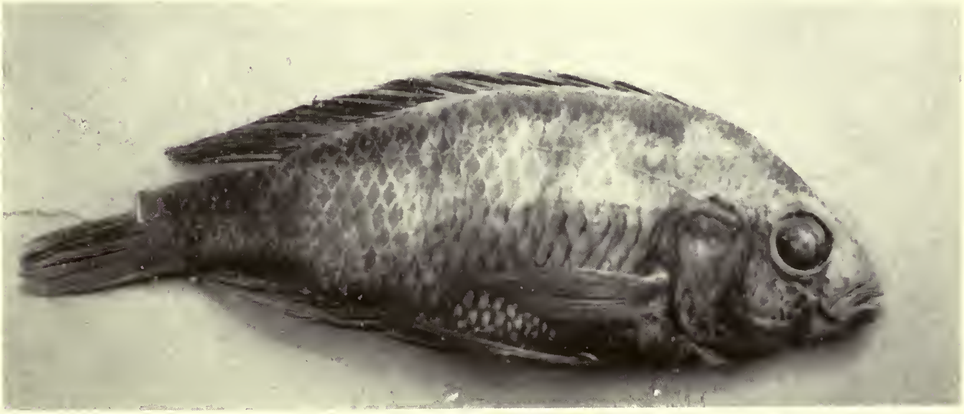
PLATE 4

The types of *Haplochromis sauvagei* (Pfeffer) upper and *H. nuchisquamulatus* (Hilgendorf) lower (see Greenwood, 1956, *Bull B.M.* (*N.H.*) *Zool.* **4**, 241), from photographs made in the Berlin Museum in 1921. Both specimens may be lost.





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A REVISION OF THE GENERA *NIDALIA* AND *BELLONELLA*

WITH AN EMENDATION OF NOMENCLATURE AND TAXONOMIC DEFINITIONS FOR THE FAMILY NIDALIIDAE (OCTOCORALLIA, ALCYONACEA)

HUZIO UTINOMI

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BY

HUZIO UTINOMI, D.Sc.

(Seto Marine Biological Laboratory, Japan)

Pp. 99–121 ; 6 *Text-figures*

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A REVISION OF THE GENERA *NIDALIA* AND *BELLONELLA*, WITH AN EMENDATION OF NOMENCLATURE AND TAXONOMIC DEFINITIONS FOR THE FAMILY NIDALIIDAE (OCTOCORALLIA, ALCYONACEA)[1]

By HUZIO UTINOMI, D.Sc.

SYNOPSIS

Redescriptions are given of *Nidalia occidentalis* Gray, *Bellonella granulata* Gray and *Bellonella* (*Cereopsis*) *bocagei* (Kent) Wright & Studer, based on types in the collections of the British Museum. A review of all the known species revealed some diagnostic characters and synonymies for the two genera *Nidalia* and *Bellonella,* which are here recognized as valid separate genera belonging to different families.

The family Nidaliidae of Gray is re-established for the generally used name Siphonogorgiidae and the reasons for this are discussed. The unbranched cylindrical Bellonellids, with somewhat contractile calyces, are shown to be essentially primitive, and from them are derived the unbranched Nidaliids and more ramose Siphonogorgiids with firm calyces, though not through the line of Nephtheidae.

The concept now outlined of the supposed evolutionary trends in the Alcyonacea is based mainly on a consideration of the retractility of polyps as a whole and is contrary to earlier ideas of evolution in the group.

I. INTRODUCTION

DURING the course of working on the octocorallian collections in His Majesty's Biological Laboratory in Tokyo, and, in particular, when reviewing the Japanese species of the so-called genus *Nidalia,* I have come to recognize a distinctive developmental tendency between the species, in spiculation and polyp structure, suggesting a supposed evolutionary trend from the Alcyoniidae to the Siphonogorgiidae. In the meantime, Mr. Frederick M. Bayer of the U.S. National Museum asked me to make a comparison between *Nidalia occidentalis* Gray, type of the genus, and the Indo-Pacific forms of " *Nidalia* ", with a suggestion that the former may be congeneric with a *Cactogorgia*-species from the Indian Ocean, formerly referred to the family Siphonogorgiidae. Subsequently to further this work the authorities of the U.S. National Museum have very kindly presented a topotypic specimen of *Nidalia occidentalis* preserved in that Museum, together with several specimens of some Nephtheid octocorals, to our Laboratory Collection.

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[1] Contributions from the Seto Marine Biological Laboratory, No. 307.

The remarkable similarity of the genus *Cactogorgia* to the older genus *Nidalia* led me to re-examine the types of *Nidalia* and *Bellonella*, both of which have been considered synonymous by most of the previous authors. Fortunately I have been able to do this through the generosity of the British Museum (Natural History) and to compare them with the Atlantic and Indo-Pacific (in particular the Japanese) forms. In connexion with this, a more critical review of the allied genera formerly placed in the families Alcyoniidae and Siphonogorgiidae was necessary. In the revision that follows, however, a number of " *Siphonogorgia* " species were either not satisfactorily classified or were left out of consideration, and, in the brief notes below, it has been thought desirable to indicate their present status, and where possible to add new information.

II. REDESCRIPTION OF *NIDALIA OCCIDENTALIS* GRAY

(Text-figs. 1–3)

The following description is mainly based upon a complete specimen presented from the U.S. National Museum and partly (spicules only) upon a fragment of the type material in the British Museum (Nat. Hist.).

Material Examined. (1) A specimen labelled as " USNM 50398 ", from *Pelican* St. 169–7 : 28° 24·5′ N., 80° 03·0′ W., east of Cape Canaveral, Florida, 45 fms. Jan. 18, 1940.

(2) Two fragments from the holotype in the British Museum, from off Montserrat, West Indies ; depth unknown.

Description. The colony from east of Cape Canaveral, Florida, is attached to a sedentary polychaete tube, on which a young colony of a Muriceid gorgonid, *Thesea grandiflora*, was also living. It is torch-like in form, consisting of a barren rigid stalk tapering downwards, and an expanded head-like polyparium covered with a number of large verrucae (more than 40) close together at the slightly convex summit. The total height is 22 mm., of which about 17 mm. belongs to the stalk proper ; the polyparium is 9 mm. in diameter and about 5 mm. high in the middle. The largest verruca at the summit of polyparium is about 1·5 mm. in diameter and about 0·88 mm. in height, and as its tip is blunt, the margin appears rounded.

The anthocodiae are completely withdrawn into the verrucae. They show a well-developed armature at their head. It consists of the eight points and a number of collaret rows transversely arranged below, both of which show considerable irregularity in the size and arrangement of spicules. In more regular arrangement the anthocodial spicules may be counted about 4–5 pairs *en chevron* in each point and up to about 15 transverse rows in the collaret.

The tentacles, which are simply infolded over the mouth in the contracted condition, are probably up to 2 mm. in length when fully exserted and bear about 7–8 pairs of long pinnules. Their aboral surface is densely packed with small, slightly roughened, rodlets which tend to be arranged *en chevron* and become larger towards the base, whereas the pinnules are apparently devoid of spicules or have a few very minute rodlets.

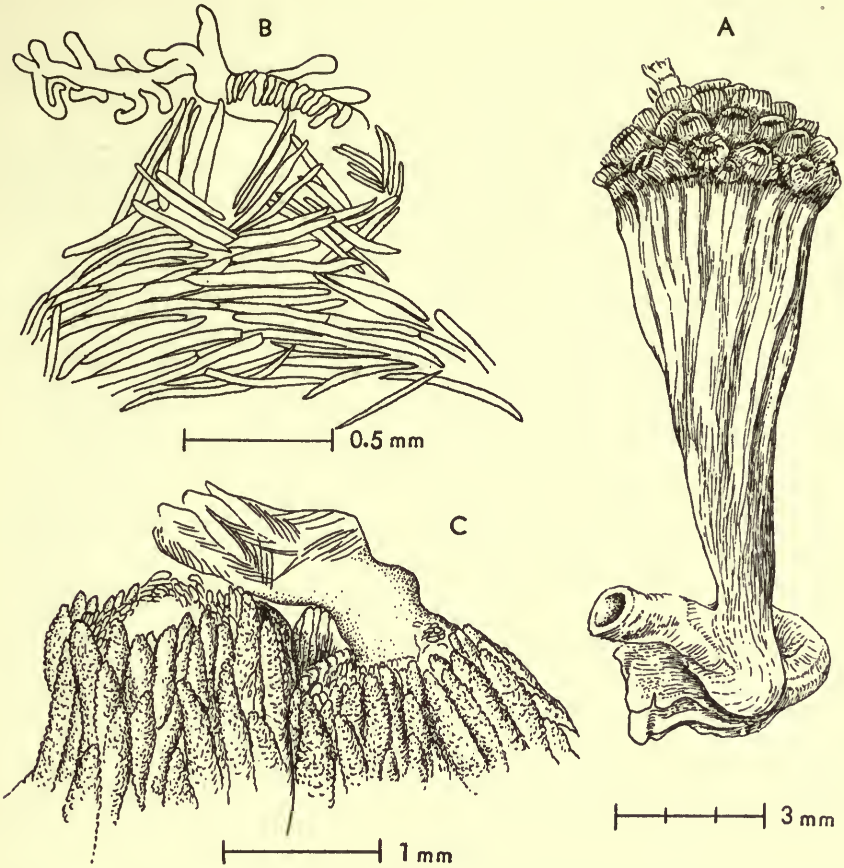

Fig. 1. *Nidalia occidentalis* Gray: A, a specimen from East of Cape Canaveral, Florida, 45 fms.; B, anthocodial spiculation in two points and in a tentacle; C, tip of two verrucae, with a polyp extended. Note a number of minute scale-like sclerites inside the tip of verrucae.

The middle part of the introvertible neck zone (" the introvert " of Deichmann) is wholly bare just below the collarets, while at its base, lining the tip of the verrucae, there are numerous very small, colourless, oval scales which are irregularly set, but roughly arranged in the eight interseptal tracts.

The verrucae, i.e., the unretracted thickened part of the polyps, are supported by very firm walls densely packed with large stout spindles similar to those of the stalk. These spicules are longitudinally disposed close together, and are not grouped in eight regions.

The stalk is deeply furrowed longitudinally on the surface due to the longitudinal arrangement of large spicules, which are all strongly tuberculated spindles up to 2·5 mm. in length, covered with compound tubercles, simply or in clusters. The coenenchyme is also densely spiculose, since the canal-walls are very compact with

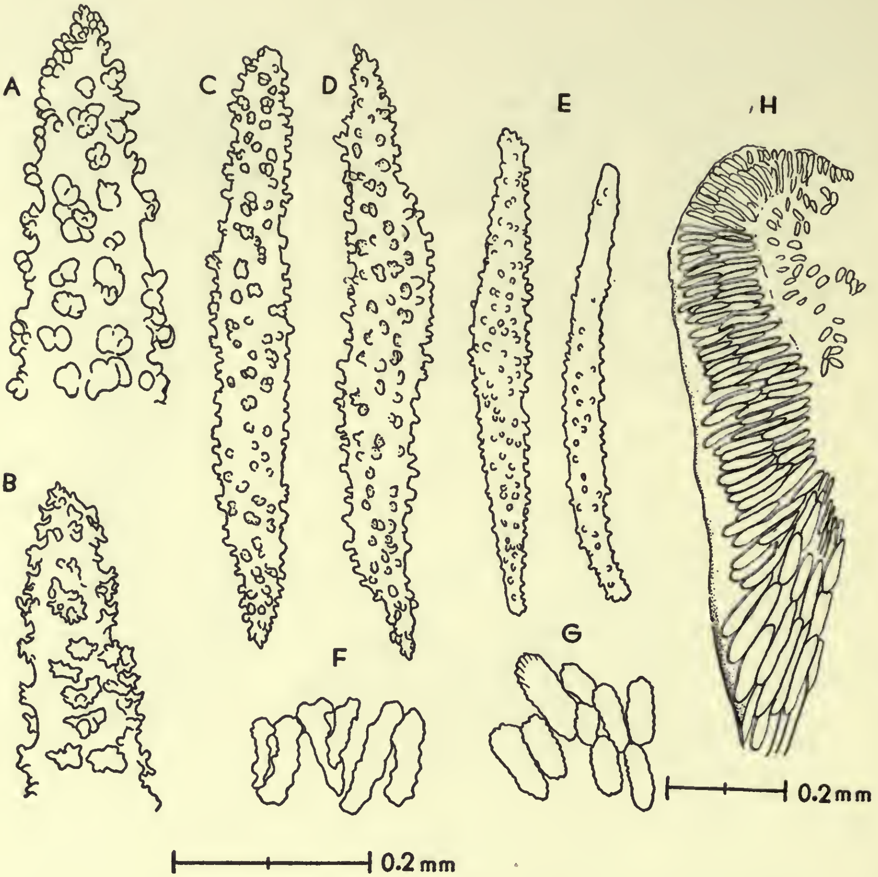

FIG. 2. *Nidalia occidentalis* Gray : A and B, part of larger spicules from stalk rind ; C, typical spindle of stalk rind ; D, typical spindle of verrucae ; E, anthocodial spiculae ; F, flat rodlets from tentacle ; G, scales from introvert ; H, side view of tentacle with dense arrangement of spicules (from the type specimen of Gray). Scale on the left applies to A–G, and that on the right to H only.

similar spindles longitudinally disposed, without any sign of the boundary or the difference in size and shape of spicules separating the interior from the surface layer.

The colour of the specimen is orange-yellow in alcohol, paler towards the base of the stalk, due to the degree of preservation of the colour of spicules themselves. The anthocodial spicules, together with those of introverts are, however, colourless.

Measurements of Spicules (in mm.).

Anthocodial spicules :

Point—warty spindles with simple warts. 0·36 × 0·035 ; 0·4 × 0·035.

Collaret—do. 0·4 × 0·05 ; 0·56 × 0·05 ; 0·6 × 0·035.

Tentacle—flat rodlets with jagged furniture. 0·1 × 0·036; 0·12 × 0·03; 0·14 × 0·028.

Introvert—scales with scalloped edges. 0·06 × 0·028; 0·075 × 0·028; 0·09 × 0·036.

Stalk spicules:

Verruca—multituberculate spindles. 1·0 × 0·23; 1·2 × 0·17; 1·5 × 0·3.

Stalk (incl. surface and interior)—do. 1·4 × 0·17; 1·5 × 0·29; 2·0 × 0·32.

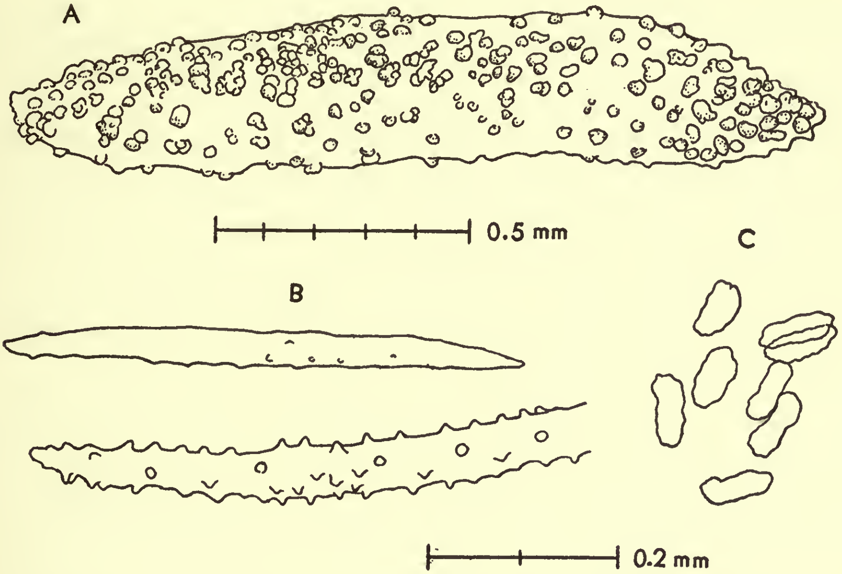

FIG. 3. *Nidalia occidentalis* Gray: A, spindle from stalk rind; B, anthocodial spindles; C, scales from introvert. All spicules from the type specimen in the British Museum (Nat. Hist.).

REMARKS. This specimen as described above corresponds exactly with the type of Gray in details of the structure and spiculation; some spicules of the latter are shown in text-fig. 3 for comparison. Deichmann (1936, p. 56) described an additional species, *Nidalia rigida*, but the two are so alike that it is not possible to separate them from each other specifically.

Cactogorgia simpsoni (taken at "Siboga" St. 289) which was fully described and figured by Thomson & Dean (1931, p. 184) is, curiously enough, in general agreement with this *Nidalia occidentalis*, in spite of the considerable distance separating their localities.

In particular, the occurrence of numerous small oval scale-like sclerites in the neck zone or "introvert", a character which had not been noted in the remaining species of *Cactogorgia*, proves the former to be identical with the latter. It is indeed wonderful that only Mr. Frederick M. Bayer (personal communication) seems to have noticed this similarity.

TYPE LOCALITY. Off Montserrat, West Indies.

DISTRIBUTION. Atlantic coast of North America and West Indies from off South Carolina to off Barbados, in 38–170 fms. (Deichmann, 1936; Bayer, 1952; 1954*a*; as *Nidalia occidentalis*); off Timor, Arafura Sea, 112 m. (Thomson & Dean, 1931, as *Cactogorgia simpsoni*).

III. REDESCRIPTION OF *BELLONELLA GRANULATA* GRAY

(Text-fig. 4)

Bellonella granulata Gray, the type species of *Bellonella*, was only briefly described from Bellona Reef, north-west coast of Australia, with only a figure of the total animal (Gray, 1862; p. 35). Since then, it has not been found again except for an enigmatic record by Thomson & Dean (1931) from "Siboga" St. 240, in the Banda Sea, at a depth of 9–45 m., which is only a moderate distance from the type locality.

As regards the spiculation, Gray mentions only that "It has some characters in common with my genus *Nidalia* but differs from it in the surface of the coral being minutely granular, and not spiculose." This very brief account led all later students, especially Kükenthal, to misinterpret the status of the genus in the classification of this group. Therefore, the re-examination and fuller description of Gray's type specimen seemed highly desirable, and this was now made possible through the re-examination of material from the British Museum.

MATERIAL EXAMINED. Spicules of type material on two mounted slides.

DESCRIPTION. The type specimen itself could not be examined by me, but, as inferred from the original figure given by Gray (1862, p. 34), the colony consists of a cylindrical stalk somewhat expanded at base and a capitate polyparium. A number of polyps, crowded together at the top of hemispherical head, apparently resembling those in the preceding *Nidalia occidentalis*, are completely retractile, and when at rest their verrucae appear 8-lobed at the tip as in most of the other *Bellonella* species, and not truncated.

The outer surface of the stalk without polyps is minutely granular according to Gray. This granular appearance depends upon the dense covering of minute spicules, some of which are figured here for the first time. The spicules are slender thorny spindles, or clubs with more spiny heads derived from spindles. The spindles are usually longer than the clubs, and they are all transparent and colourless, though some retain still a slightly rosy hue around the axis (see Text-fig. 4B).

According to Gray, "the base of the polyps is strengthened with very minute spicula, placed in a longitudinal series parallel to each other." These spicules are also transparent, slightly rosy to yellowish in colour and somewhat club-like in form, bluntly headed (see Text-fig. 4A).

Measurement of Spicules (in mm.).

Stalk spicules:

Spindles—0·17 × 0·04; 0·25 × 0·07; 0·28 × 0·05; 0·32 × 0·035.

Clubs—0·1 × 0·05; 0·14 × 0·05; 0·17 × 0·05; 0·25 × 0·05.

Polyp spicules:

Clubs—0·16 × 0·035; 0·19 × 0·05; 0·25 × 0·05; 0·28 × 0·05.

REMARKS. According to Thomson & Dean (1931), a small specimen, taken at

" Siboga " St. 240, which was recorded under the name " *Nidalia granulata* (Gray) " is about 1·5 cm. in height, with a maximum diameter of 5 mm. and ochraceous in colour. The coenenchymal spicules are said to be " minute double spheres, knobbed capstans, a few warty rods " and practically no spindles are included. It is thus beyond doubt that they have erroneously identified this specimen, without making reference to the type specimen. Their description without figures is too inadequate to permit any other suggestions.

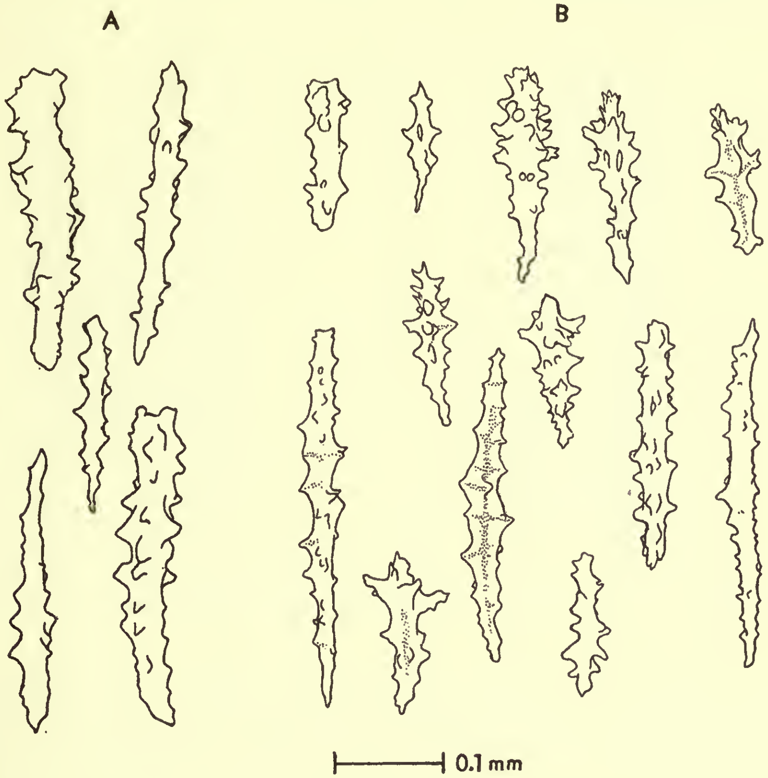

FIG. 4. *Bellonella granulata* Gray : A, spicules from the polyps ; B, spicules from the stalk. All spicules from the type specimen in the British Museum (Nat. Hist.).

DISTRIBUTION. Type locality only—Bellona Reef, north-western coast of Australia, 17 fms.

IV. REDESCRIPTION OF *BELLONELLA BOCAGEI* WRIGHT & STUDER

(Text-figs. 5–6)

The following description is based on fragments of the material of *Bellonella bocagei* (Kent), collected by the *Challenger* from the west of Azores, and now in the collections of the British Museum.

Description. The specimen is excellently figured by Wright & Studer (1889, p. 241; pl. 37, fig. 2) as here reproduced in text-fig. 5A, but their description is not sufficiently detailed for recognition of the species.

The specimen figured forms a cylindrical colony arising from a flat extended base. As measured from the original figure, it rises from the base to a height of about 6 cm., with a diameter of about 8 mm. in the middle of the stalk. The upper half is rather loosely covered with large cylindrical polyps, and the lower half is apparently bare, bearing no polyps at all.

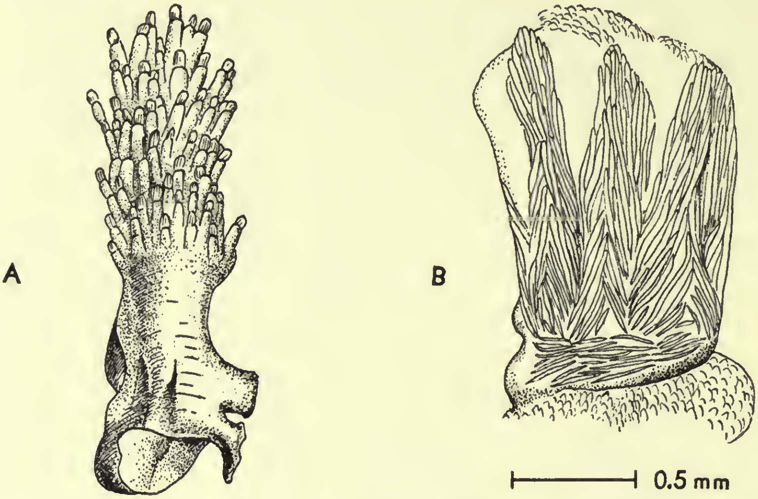

Fig. 5. *Bellonella bocagei* (Kent): A, a *Challenger* specimen (redrawn from Wright & Studer, 1889); B, anthocodia with partially contracted anthostele.

When extended, the polyps may attain a length of about 2 mm., with a diameter of about 0·8 mm. at the head. At the base each forms an 8-lobed, low verruca which is thick-walled and spiculiferous. The tentacles bear slender, curved or spiny, flat rodlets on the aboral side. The anthocodial armature consists of 8 double rows of steeply-converging slender spindles with low warts and bluntly ended. Below these the similar spindles are arranged in about 10 transverse rows, and they become sparser and smaller in size in the eight interseptal tracts of the neck zone down to the basal calyx (Text-fig. 5B).

The stalk cortex is closely packed with long, spiny spindles or shorter, spiny clubs thickened at upper end. The coenenchyme contains more slender spindles with high warts.

All these spicules are usually transparent and colourless, but some reddish ones are found on the cortex of polyparium.

Measurements of Spicules (in mm.).

Anthocodia—0·25 × 0·05; 0·35 × 0·05 (Text-fig. 6A).

Tentacle—0·09 ~ 0·14 × 0·01 ~ 0·02 (Text-fig. 6B).

Neck zone—0·035 ~ 0·055 × 0·01 ~ 0·03 (Text-fig. 6C).

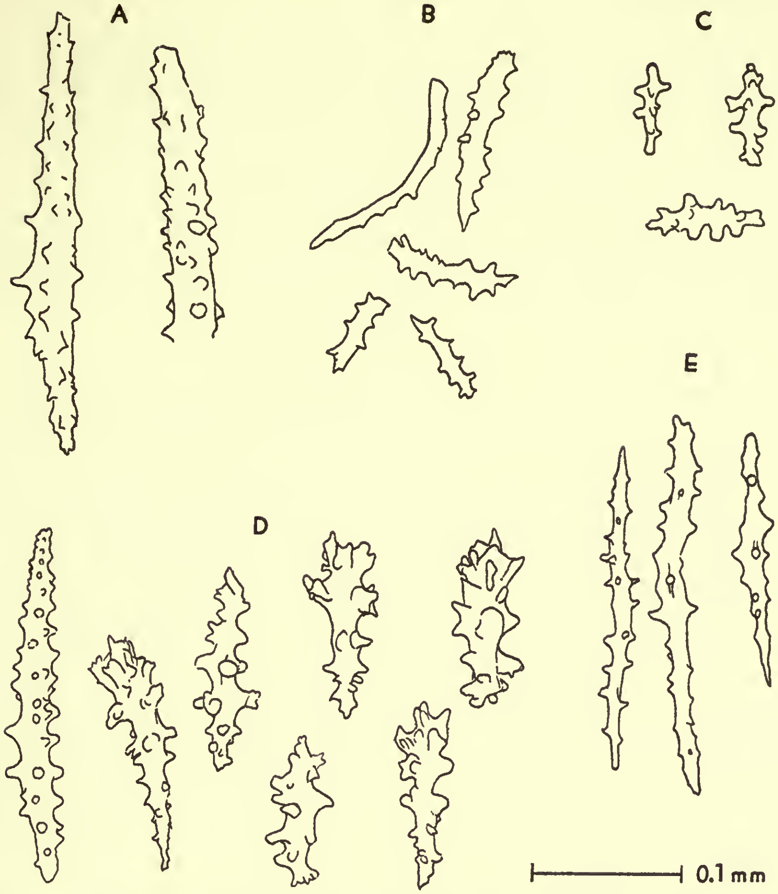

FIG. 6. *Bellonella bocagei* (Kent) : A, anthocodial point spicules ; B, tentacle spicules ; C, spicules from neck zone ; D, spicules from stalk rind ; E, coenenchymal spicules in canal-walls, All are drawn from a specimen in the British Museum (Nat. Hist.).

Stalk cortex—0·09 × 0·035 ; 0·12 × 0·05 ; 0·23 × 0·035 (Text-fig. 6D).
Coenenchyme—0·09 ~ 0·25 × 0·009 ~ 0·017 (Text-fig. 6E).

REMARKS. This species was originally described by W. Saville Kent (1870, p. 398) under the name *Cereopsis Bocagei* gen. nov. et sp. nov., from specimens taken off Setubal, Portugal in 15 fms. Wright & Studer (1889) identified this specimen with Kent's species and transferred it to Gray's genus *Bellonella*, together with *Nidalia atlantica* Studer (1878, p. 635) and *Itephitrus*[1] *speciosus* W. Koch (1886) recorded from the neighbouring waters as synonyms. This procedure was followed by Pütter (1900) who reviewed the hitherto known species of *Bellonella*. Most of the later authors, however, regarded this species as a member of *Gersemia* (Kükenthal,

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[1] Erroneously called *Iphethyrus* or *Iphythyrus* by Wright & Studer and May respectively.

1906*a*, *b*, 1907; Thomson, 1927) or as a member of *Alcyonium* (Molander, 1915; Deichmann, 1936).

Apart from a problem concerning the distinction between the families Alcyoniidae and Nephtheidae from which such different opinions were probably derived, I came to the conclusion, by a close comparison of all Japanese species of *Bellonella* with other related genera of both families, that its assignment to the genus *Bellonella* is highly advisable as proposed by Wright & Studer.

DISTRIBUTION. Off Setubal, Portugal, 15 fms. (Type locality); off Senegal, tropical West Africa, 115 fms. (" Gazelle " St.); west of the Azores, 450 fms. *Challenger* St.; Rolas, Gulf of Guinea; Azores, 845 m.[1] (" Prince Albert I " St. 584).

V. VALIDITY OF THE GENUS *BELLONELLA* AND ITS SYNONYMY

As mentioned above, the genus *Bellonella* was created by Gray (1862) for a single species *B. granulata*, and later (1869) placed in his family Bellonelladae near the Xeniidae. At that time he recognized an obvious difference in spiculation separating it from his earlier genus *Nidalia* although he did not go into details.

His systematization of various octocorallian genera has not, in general, been accepted in modern systems of classification, and his views on the distinguishing characters between *Bellonella* and *Nidalia* have been opposed by most later authors. Wright & Studer (1889) at first suggested the probable identity of both the genera, though actually treating them separately. In recent years the two genera have been united by May (1900), and in particular, by Kükenthal (1906*a*, *b*), who was convinced that some species contained in the genus *Bellonella* (*Nidalia* in his sense) should be retained in the Alcyoniidae, while others like *Gersemia* and *Capnella* should be transferred to the Nephtheidae.

Among recent authors, only J. S. Thomson (1910, 1921) expressed a doubt as to whether Gray's *Nidalia* and *Bellonella* are really identical, and referred two South African species to the latter genus as *B. studeri* n. sp. and *B. rubra* Brundin. In addition to these, he recognized Pfeffer's *Metalcyonium* as a distinct genus from *Bellonella*, referring three species to it.

Prior to him, Kükenthal (1906*a*) divided the genus *Alcyonium* Linnaeus into three subgenera, *Alcyonium* s. str., *Metalcyonium* and *Erythropodium* (later changed as *Parerythropodium*). Although this attempt has not been followed by most other authors, especially Molander (1915), it is undoubted that *Metalcyonium* is a unique group embracing the species which are clavate, capitate or mushroom-shaped and ordinarily unbranched in form. Most of them were known from the subantarctic region (Patagonia and South Africa), but later a few were recorded from Amboina, East Indies (Burchardt, 1902) and northern Japan (Yamada, 1950).

Judging from the descriptions given by Pfeffer (1889) and Kükenthal (1906*a*), and also from photographs published by Molander (1929, pl. IV, fig. 9), *Metalcyonium clavatum* Pfeffer, which is the type of the genus, seems to be very different from others since referred to the genus (or subgenus) in its form of growth. Although I have no personal knowledge of this species, its close affinity with the genus *Bellonella* cannot be denied.

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[1] Thomson's identification is still in doubt (*see* Deichmann, 1936; p. 51).

Kükenthal (1906*a*, *b*), in dividing the family into two subfamilies, Nidalliinae (*sensu* Kükenthal) and Alcyoniinae, emphasized that the canal system is direct and partly indirect in the former, while indirect in the latter. Such a difference was, however, strongly rejected by Molander (1915).

According to Molander, *Metalcyonium clavatum* often shows a sign of slight division of the polyparium into side branches (or lobes). Here I only wish to point out that on investigating the Japanese species of *Bellonella* such examples as *M. clavatum* could be observed normally or abnormally (Utinomi, 1957).

Even if this *M. clavatum* can be regarded as belonging to *Bellonella* on account of the unbranched cylindrical form of growth, this cannot be applied to other mushroom-like forms such as *M. capitatum* Pfeffer, *patagonicum* May, *molle* Burchardt and *novare* Kükenthal, as well as other unbranched alcyoniids tentatively referred to the genus *Alcyonium* in the widest sense (for example, see J. S. Thomson, 1910 ; Yamada, 1950 and Tixier-Durivault, 1954).

If this re-grouping is actually justified as limited by the type designation for Pfeffer's genus *Metalcyonium*, these capitate forms are left without a genus and therefore require a new genus or subgenus name. But for the present, the differences between these unbranched, either cylindrical or capitate, forms of *Metalcyonium* and many of lobate or branched forms of the true *Alcyonium* s. str. are so vague, that only by a complete revision can their status be decided.

In this revision below, though admittedly not complete, the position of the species which have been referred to *Nidalia* (*Bellonella*) or other genera is considered chronologically and the conclusion reached earlier for others are re-stated briefly.

Bellonella granulata Gray (1862) is designated by monotypy as the type of a valid genus *Bellonella* Gray, 1862.

Cereopsis Bocagei Kent (1870) is, as mentioned above, referable to *Bellonella*, following Wright & Studer (1889) and May (1900). Its assignment to either *Alcyonium* or a Nephtheid genus *Gersemia*, as proposed by later authors, is not adequate.

Another species *C. studeri*, described by von Koch (1891) from Naples, Italy, was referred to *Nidalia* by May, and then to *Gersemia* by Kükenthal. This species was later re-discovered and fully described by Thomson & Dean (1931) from the East Indies and by Stiasny (1941) from Naples, under the original name. Very recently I had a similar specimen, referable to this species, from Sagami Bay, Japan (unpublished) and noted some remarkable characters generically distinguishable from the type species of *Cereopsis*. Therefore, the genus name *Cereopsis* cannot be used for both *bocagei* and *studeri* as a synonym of *Bellonella*, though it was later replaced by the substitute name *Cereöpsida* Strand (1928). Koch's *studeri* appears to be generically distinct from the type species *bocagei*, and therefore requires a new genus, for which the new name **Kochella** is here proposed. Detailed discussion as to this form will appear in another paper.

Nidalia atlantica Studer (1878, p. 635)

Itephitrus speciosus W. Koch (1886, p. 1)

Both species are probably synonymous with *Bellonella bocagei* (Kent), together with the *Challenger* specimen described above.

Nidalia arctica Danielssen (1887, p. 119)
This species, together with *Organidus nordenskjöldi* and *Krystallofanes polaris* succeedingly described in the same paper, are probably not Bellonellids but may be merely young or stunted specimens of *Gersemia fruticosa* (Sars) (= *G. rubiformis*, *sensu* Madsen, 1944).

Bellonella variabilis Studer (1901, p. 25)
(= *Rhodophytum variabile* Studer, 1890, p. 89)
Kükenthal (1906*a*, *b*) referred this species to *Gersemia*, but Molander (1915) who studied Studer's original type, and Deichmann (1936) consider it a stunted specimen of *Alcyonium glomeratum* Hassall with the least development of polypiferous lobes.

Bellonella rubra Brundin (1896, p. 6)
Bellonella cinerea Brundin (1896, p. 8)
Both species first recorded from Japanese waters distinctly belong to *Bellonella*. The identity of the latter with the former, as proposed by Kükenthal, is still open to question and must await the discovery of more material.

Bellonella rigida Pütter (1900, p. 448)
Eleutherobia japonica Pütter (1900, p. 449)
The latter is undoubtedly a synonym of the former. This is a sand-dwelling form, where the stalk is often rounded at the base, apparently as in the pennatulids, such as *Cavernularia* and *Veretillum*. In fact, Thomson & Rennet (1927, p. 143) carelessly included it in the report on the Japanese species of pennatulids.

Nidalia foliacea May (1900, p. 101)
Probably identical with a Nephtheid *Capnella imbricata* (Quoy & Gaimard).

Bellonella indica Thomson & Henderson (1905, p. 274)
Probably a valid species with coenenchymal spicules of capstan type.

Bellonella studeri J. S. Thomson (1910, p. 550)
Bellonella rubra Brundin (J. S. Thomson, 1910, p. 554)
Metalcyonium clavatum Pfeffer (J. S. Thomson, 1910, p. 556)
These three species recorded from South Africa are probably valid species of *Bellonella*. But the second species may be different from the species occurring in Japan. According to Molander (1929), the third is not the same as the typical species from South Georgia.

Nidalia rubra (Brundin) (Tixier-Durivault, 1954 ; p. 127)
Nidalia morifera Tixier-Durivault (1954, p. 128)
The former, though briefly described, may be similar to the species of the same name from South Africa, which is mentioned above. The latter is a peculiar *Bellonella*, closely resembling *B. grayi* (Thomson & Dean, 1931) in having an indistinct sterile stalk and in having no spicules in the anthocodiae.

Apart from these, a number of new species have been described by Kükenthal (1906*b*), Nutting (1912) and Thomson & Dean (1931), all referring to *Nidalia*. The majority of them should be placed in the genus *Bellonella* as valid species, but only a direct comparison with their types will decide it. Further information as to the synonymies and affinities is given in my recent paper reviewing Japanese species of *Bellonella* (Utinomi, 1957).

Consequent upon re-examination of the types of both *Nidalia* and *Bellonella* and a review of all previous records referred to both genera and related genera, a revised diagnosis of the genus *Bellonella* Gray is given below :

DIAGNOSIS. Alcyoniids whose colonies are cylindrical or subcylindrical. Colony with a stalk and an unbranched (scarcely slightly-lobed) cylindrical polyparium. Polyps large, monomorphic, fully-retractile within 8-lobed, or truncated, calyces. Gastric cavities of all polyps closely fascicled, extending to base. Anthocodiae, with or without, 8-chevroned rows of spicules. Coenenchymal spiculation sparse but dense in outer cortical layer. Spicules : spindles, rods, clubs and capstans. Usually vividly coloured. Living in deep waters of all the oceans.

Type species : *Bellonella granulata* Gray (1862).

VI. SYSTEMATIC POSITION OF THE GENUS *NIDALIA* AND ITS RELATIONSHIP WITH SIPHONOGORGIIDS

The genus *Nidalia* was erected by Gray (1835) to contain a single species, *N. occidentalis*, from off Montserrat, West Indies. The original description given by Gray is quite insufficient for the diagnosis of the genus and species, and there was no figure or description of the spicules. Accordingly, regrettably enough, Studer (1901) and Kükenthal (1906*a*, *b*) merged the genera *Nidalia* and *Bellonella* as synonymous. The former authority used the name *Bellonella*, while the latter on the contrary the older name *Nidalia* as the generic name. Nevertheless, Kükenthal actually neglected to consider the name of *Nidalia occidentalis*, which is the type species, in recording all of the hitherto known and undescribed species of the genus (*Nidalia* or *Bellonella*). It is possible that he might have denied its actual existence. This confusion might be due to the lack of exact knowledge of both the types, and the superficial resemblances of the colonies, based mainly on the imperfect descriptions of Gray.

Since the original descriptions, both the type species were not found again for many years. Deichmann (1936) was apparently the first to recognize *Nidalia occidentalis* as a distinct species and genus. At the same time she described another species (*N. rigida*), but her species cannot be regarded as distinct and she did not put forward any further comparison with the Indo-Pacific forms of " *Nidalia* ". Accordingly, more recent workers, including myself, have followed Kükenthal in considering *Bellonella* a synonym of *Nidalia*.

As has already been remarked in the preceding chapters, *Nidalia occidentalis* Gray differs considerably from *Bellonella granulata* Gray and the allied forms. The differences justify separating the two as different genera and even different families, the former as a member of " Siphonogorgiidae ", and the latter to the Alcyoniidae.

The diagnostic salient characteristics of *Nidalia occidentalis* may be summarized below :

The colony is torch-like (instead of cylindrical in a strict sense), unbranched, with an expanded hemispherical capitulum covered with large crater-like calyces. Calyces are not 8-lobed, but are truncated at the tip, and thick-walled, being closely packed with large, multituberculate spindles arranged longitudinally. Coenenchymal spiculation in the stalk is more rigid, giving the whole colony a brittle consistency.

These characters indicate its closest affinity with the " Siphonogorgiidae " amongst families of the Alcyonacea.

In searching in literature I have not seen it mentioned in any paper, where it might be expected to be found. As mentioned above, only Mr. Frederick M. Bayer (personal communication) seems to have been aware of a remarkable similarity between *Nidalia occidentalis* and *Cactogorgia simpsoni*.

The genus *Cactogorgia* was established by Simpson (1907; see also, Thomson & Simpson 1909, pp. 143–150) for three species, showing different growth forms, collected by the R. I. M. S. ship *Investigator* in the Indian Ocean. They are *C. celosioides* from Andamans (depth unknown), *C. expansa* from off Cape Comorin in 38 fms. and *C. alciformis* from Andamans and off Arakan coast from 13 fms. Since then, three more species have been recorded, also from the Indian Ocean. They are *C. lampas* Thomson & Mackinnon (1910) from the Seychelles from 37 fms., *C. agariciformis* Simpson (1910) from an unknown locality and *C. simpsoni* Thomson & Dean 1931) from " Siboga " St. 289 (9° 0·3′ S., 126° 24·5′ E., 112 m., SE. of Timor).

Notwithstanding the differences in the shape of the colony and the anthocodial armature, all of these species agree well with one another in not having any definite branching and in having a marked distinction into sterile trunk and polyp-bearing portion, and in showing dense spiculation of the canal-walls, as well as in the rind. In addition, all spicules are very large, stout, highly-tuberculate spindles of the *Siphonogorgia*-type, and the tentacle spicules are minute, scale-like; the anthocodiae show the definite " crown and points " armature arrangement and are completely retractile within the thick-walled verrucae, as in *Nidalia occidentalis* and many of *Siphonogorgia* species. They are generally yellow to orange coloured. Therefore I do not hesitate to regard the two genera as congeneric, and in doing so note that *Nidalia* has priority over *Cactogorgia* as the generic name.

As regards the systematic position of this *Cactogorgia* and also *Agaricoides* (Simpson, 1905; Thomson & Henderson, 1906), opinions differ between the British and German authorities. Originally Simpson placed both among the Siphonogorgiinae (as a subfamily of the Nephtheidae) on account of the rigid consistency of the colony caused by the dense spiculation in the coenenchyme. Among recent authors, for example, Chalmers (1929), Hickson (1930) and Bayer (1956) consider that they are more closely related to the family Siphonogorgiidae than to any other.

Kükenthal (1896) raised the subfamily Siphonogorgiinae to the rank of a separate family as Siphonogorgiidae in the belief that *Siphonogorgia* is intermediate in form between the Nephthyidae (= Nephtheidae) and the Gorgoniidae (= Gorgonacea, in particular, Scleraxonia). Nevertheless, later (1906*b*, 1910) he pointed out the dissimilarity of Simpson's two new genera to the gorgonids, suggesting only a near relationship of *Agaricoides* to *Nidalia* (= *Bellonella*) *macrospina* Kük. and that of *Cactogorgia* to *Nidaliopsis pygmaea* Kük., both belonging to the Alcyoniidae.

From an examination of *N. macrospina* from Japan Kükenthal's suggestion is amply confirmed. In this connexion, a note by Thomson & Simpson (1909, p. 135) recalls that *Siphonogorgia annectens* n. sp. " bears a strong resemblance to *Nidalia macrospina* Kükenthal." This siphonogorgiid is, according to Macfadyen (1936), probably synonymous with *Nephthyigorgia pinnata* which genus was created by Kükenthal (1910) for three Australian species showing a poor internal spiculation in the stem. This view also may possibly be right.

If these closer relationships to either of the two families Siphonogorgiidae and

Alcyoniidae (instead of Nephtheidae as generally accepted) are actually justified, then we are faced with the alternatives of expanding the definition of either of the two families generally accepted or erecting a new separate family for these unbranched forms.

A search of the literature on *Siphonogorgia* Kölliker (including *Chironephthya* Wright & Studer), comprising a large number of species, reveals that the hardness of coenenchymes due to the dense internal spiculation, given by Wright & Studer (1889) as diagnostic, is quite untenable. As can be deduced from a list of hitherto known species of *Siphonogorgia* given by Thomson & Dean (1931, pp. 153–166), the coenenchymal spiculation especially in the canal-walls is very variable, and in another closely related genus, *Nephthyigorgia*, the distribution of spicules is largely confined to the outer layer (usually called cortex or rind).

The rigid consistency and brittleness of the colony which characterize *Siphonogorgia* and allied genera are mainly due to the thick wall formed by a definite close arrangement of longitudinally-disposed, large spindles, regardless of internal spiculation whatever. Therefore, the colonies are decidedly different structurally from those of the Gorgonacea, since no spicular axis as seen in the Scleraxonian gorgonids is formed in the interior, although there may be a superficial resemblance in the mode of growth.

In both the genera mentioned above, *Nidalia* (*Cactogorgia*) and *Agaricoides*, the colonies are generally unbranched, like alcyoniids such as *Bellonella* and *Anthomastus*, but the spiculation of the cortex and the structure of polyps are more closely related to the Siphonogorgiidae than to the Alcyoniidae. Thus it seems better to include both under the former group as a special subfamily rather than to erect a separate family.

In doing so, however, the generally used family name Siphonogorgiidae (*pro* Siphonogorgiaceae Kölliker, 1875, p. 22) should be displaced by the name Nidaliidae (*pro* Nidalidae Gray, 1869, p. 127), since the latter has priority over the former as the family name. Gray's diagnosis, that is " Coral simple or branched ; stem cylindrical, cartilaginous, with a crustaceous skin and imbedded spicules. Polypes on the upper surface of a hemispherical head, with prominent large conical polype-cells ; stem and polype-cells covered with fusiform spicules " is applicable to this family without much alteration of diagnostic characters.

Below I propose a new system of classification based on the revised examination of the type specimen of *Nidalia* and reconsideration of the diagnostic characters of the allied genera, formerly assigned to the Siphonogorgiidae, in recognition of the distinctive evolutionary trends they display.

Family NIDALIIDAE Gray, 1869

Nidalidae Gray, 1869, p. 127.

Siphonogorgiaceae Kölliker, 1875, p. 22 ; Klunzinger, 1877, p. 48 (as subfamily of Alcyonidae in Alcyonacea).

Siphonogorginae Wright & Studer, 1889, p. 226 ; Thomson & Henderson, 1906, p. 11 ; Thomson & Simpson, 1909, p. 124 (as subfamily of Nephthyidae).

Siphonogorgiidae Kükenthal, 1896, p. 133 ; May, 1900, p. 171.

Siphonogorginae (*sic*) Hickson, 1903, p. 487 (ranked however as a family).

Siphonogorgiidae Kükenthal, 1906*b*, p. 68 ; Harrison, 1909, p. 31 ; Hickson, 1930, p. 244 ; Thomson & Dean, 1931, p. 149 (part) ; Bayer, 1956, p. 188 (part).
Not Nidaliinae Kükenthal, 1906*a*, p. 29 (as subfamily of Alcyoniidae).
Not Nidalinae (*sic*) Kükenthal, 1906*b*, p. 19 (as subfamily of Alcyonidae).

Emended Diagnosis. Colonies unbranched or tree-like, branched with stiff, cylindrical branches. Outer surface very roughened, closely-packed with large, multi-tuberculate spicules longitudinally-disposed, which give the colony a rigid brittle consistency. Anthocodiae completely or partially retractile, within densely spiculose tubulo-conic verrucae, more or less projecting above the surface. Anthocodial armature with symmetrical " points and crown " arrangement.

Subfamily Nidaliinae nov.

Unbranched, or slightly branched only at base ; colonies with a marked distinction into trunk and polyp-bearing portion ; densely spiculose throughout ; polyps completely retractile.

For the present, only two genera *Nidalia* Gray (= *Cactogorgia* Simpson) and *Agaricoides* Simpson are known as belonging to this subfamily.

Subfamily Siphonogorgiinae Kölliker

Profusely or feebly branched, tree-like colonies not distinctly separable into trunk and polyp-bearing branches ; canal-walls filled, densely or loosely, with spicules similar to those of rind ; polyps singly or closely-arranged on stem and completely or partially retractile.

Siphonogorgia Kölliker is a representative genus among this group. *Nephthyigorgia* Kükenthal is also probably distinct, but *Dactylonephthya* Thomson & Simpson seems unique in the absence of distinction between the anthocodiae and verrucae, if this proves to be correct. Here it is tentatively placed near the position of *Siphonogorgia*, but its re-discovery is much needed.

The remaining genera, such as *Scleronephthya* Wright & Studer and *Stereacanthia* Thomson & Henderson, if distinct as genera, may be grouped within the Nephtheidae, together with *Capnella* (= *Paranephthya*) and *Lemnalia*.

VII. EVOLUTIONARY INTERRELATIONSHIP BETWEEN ALCYONIIDAE AND NIDALIIDAE (SIPHONOGORGIIDAE AUCT.)

Our knowledge of the interrelationships of various groups and their evolutionary trends in the Alcyonaria is very incomplete. Kükenthal (1906*a*) has discussed the evolution of the Alcyonacea, concluding that the Siphonogorgiidae are the most evolved group derived from a supposed solitary *Haimeia*-like ancestor along a line Cornulariidae-Xeniidae-Alcyoniidae-Nephtheidae. But this monophyletic view has not been supported by later workers (in particular, Molander, 1915). Within the Alcyoniidae, Molander supposed two different lines of evolution as regards polyp dimorphism (one includes the monomorphic forms, and the other, the dimorphic forms) and thought that *Nidalia* (*sensu* Kükenthal) was the most primitive genus. His view seems to me adequate, but he did not extend his views to mention any further evolutionary lines along which they may have evolved.

As discussed above, *Bellonella* (namely, *Nidalia sensu* Kükenthal) is more primitive than the lobated or ramified forms of *Alcyonium* for reasons already given, and it is among this genus that we have to look for forms resembling the ancestral retractiel stoloniferans. *Nidalia* (*sensu* Gray), on the contrary, is a more advanced or specialized form to be placed near *Siphonogorgia*, although it is ordinarily unbranched in its mode of growth.

The two genera have been treated as synonymous for many years, perhaps because of the lack of true knowledge of the original types of the two, or of confusion with regard to the species status due to the superficial resemblance of the colonies.

The most primitive forms, such as *B. rubra* and *B. grandiflora*, retain the flaccid consistency of the coenenchyme, of which canal-walls are thick but not so densely spicular as in the rind. The coenenchymal spicules are of uniform shape and small in size, and the anthocodial armature retains many ancestral features seen in stoloniferans. The retractile polyp is very large, supported by a long stalk with flexible armature of small spicules continued downwards as 8 interseptal areas, so that, in contraction the short stiffened lower part of the polyp itself, called anthostele, is infolded to cover over the retracted anthocodia, forming a 8-lobed wart-like operculum by which the mouth is completely closed.

In these species showing the 8-lobed anthostele (" calyx "), the arrangement of spicules on the surface is ordinarily continuous between the anthocodia and anthostele, although sometimes interrupted by reducing spicules in the neck zone, and the anthostele is more or less contractile, and thus functional as an operculum of the polyp itself.

In the more evolved species such as *B. sibogae* (= *B. macrospina* Thomson & Dean) and *B. macrospina* (= *Nidalia macrospina* Kükenthal), the cortical spiculation is more massive and rigid, with greater stoutness of spicules. The polyps (more properly the anthocodiae), on the other hand, shorten the stalk, reduce the spicular armature in the introversible neck zone, and become heavier than the anthocodial armature.

Consequently, the discontinuity between the anthocodia and the anthostelar region in spiculation may become more pronounced and a thick-walled, non-contractile calyx as a tubular upgrowth from the cortical coenenchyme (or rind) results. The calycinal spiculation is not arranged interseptally and the apical orifice cannot be completely closed. Here the anthocodia itself, protected by spicular armature, takes a part as an operculum, as is usual in most siphonogorgiids and gorgonaceans. For further details on the evolutionary trend within the genus *Bellonella*, see Utinomi (1957).

In the genus *Siphonogorgia* the arrangement of anthocodial armature is variable between species, as pointed out by Chalmers (1929) in discussing the evolution of species within the genus. It is also probable that this arrangement is intimately concerned with the retractility of the anthocodiae.

As regards the origin of *Siphonogorgia*, in establishing the genus, Kölliker (1875) regarded it as intermediate between the Alcyonacea and the Gorgonacea in modern systems of classification. Since then, following him, most later authors generally consider that *Siphonogorgia* and allies are derived from the Nephtheidae or at least more related to it than to any other families, a conclusion from which I must most emphatically dissent. The generally accepted ideas, in particular Kükenthal's, that may have been derived from considering its Nephtheid-like mode of growth, associated with the heavier coenenchymal spiculation, and its warm-water distribution restricted to the Indo-Pacific, also appear to be untenable.

The growth form of the colony is, I believe, of limited significance in assessing whether a particular form is primitive or advanced, but reflects general trends in the group. This may reflect the effects of the external environment, especially of water movements, sea temperature and kind of substratum, although there are certain basic characteristics which are apparently never modified by the environment. Thus, such a slight sign of branching in *Nidalia occidentalis* as reported by Gray, as well as a few indistinctly-lobed examples in some species of *Cactogorgia*, suggests a probable evolutionary trend towards ramified siphonogorgiids.

In most of the genera within the family Nephtheidae, the polyps, distributed scatteredly or in groups on branches, are ordinarily not retractile, forming prominent calyces without clear division between the anthocodia and anthostele, and consequently calycinal spicules are completely continuous with those of the cortical coenenchyme of branches and stems. Each polyp is either cylindrical or clavate in shape. In the latter the spicules in the anthocodial region are somewhat bilaterally symmetrical in arrangement, instead of being radial as in most alcyoniids.

The retractile polyps in *Gersemia* and *Paralemnalia*, as in a few exceptional cases, are in all probability a secondary outcome due to the weak development of spiculation in the neck zone. Similar trends as discussed above may probably be observed also within the Gorgonacea.

As regards another aberrant family called Viguieriotidae Bayer (1954*b*), better known as Fasciculariidae Viguier, I have no personal knowledge at present. But it is likely that this family may be a complex of allied forms, having in common only a densely spiculose stalk (" cup " or " involucre ") into which retract numerous polyp-bearing lobes or branches. In other respects they are not related to one another, since one *Viguieriotes* (= *Fascicularia* Viguier) (the simplest) is closely related to the Clavulariidae, one (*Paralcyonium*) to *Bellonella* or *Nidalia*, whereas the remaining one (*Studeriotes*) is more specialized with *Nephthea*-like ramified twigs and polyp armature. Even if these genera may seem to have originated in different ways, there are insufficient reasons for refusing to combine them into a special family.

In conclusion, it need only be mentioned that the retractibility of polyps is indeed one of the important characteristics originally bestowed on the Octocorallia and even all anthozoans. It is a pity that most octocorallian specialists did not lay enough stress on this peculiar character in recognition of various groups within the Octocorallia and their evolutionary trends.

VIII. ACKNOWLEDGMENTS

I am very much indebted to the Trustees and Dr. W. J. Rees of the British Museum (Natural History) for the gift of some fragments from the Gray's type specimens and some alcyonarians in the *Challenger* Collections mentioned in the text and for much help in publishing this paper. I am particularly indebted to Mr. Frederick M. Bayer of the U.S. National Museum, Washington, for his helpful suggestion and criticism and also for many duplicated specimens sent to me for comparison. I wish to extend my sincerest thanks to Dr. Hirotaro Hattori for the privilege of studying His Majesty's vast collections to which I owe the opportunity to begin the study of the group.

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Pp. 123–161, *Plates* 5–6 ; 10 *Text-figures*

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EAR PLUG LAMINATIONS IN RELATION TO THE AGE COMPOSITION OF A POPULATION OF FIN WHALES (*BALAENOPTERA PHYSALUS*)

By P. E. PURVES and M. D. MOUNTFORD

SYNOPSIS

1. The method of grinding the ear plugs of Fin Whales and of counting their laminae is briefly described.
2. The growth of the plug is compared with that of the skull width and body length.
3. A provisional rate of formation of the laminae is assessed and correlated with previously established data about the growth and age of Fin Whales.
4. From the age frequency distribution based on the ear plug lamination analyses the apparent natural mortality rate for the " Sanctuary " population is demonstrated.

In the course of a detailed description of the ear plug of the Mysticeti (Purves, 1955) it was suggested that there might be a correlation between the laminar structure of the core of the plug and the age of the animal from which it was taken. Further support was given to this hypothesis by the examination of 18 Fin Whales at Steinshamn, Norway, during the summer of 1955, when the age as estimated from the ear plugs was compared with that assessed from the ovaries and baleen plates, Laws & Purves (1956), Ruud (1945).

The results of this enquiry were sufficiently encouraging to warrant further investigation. Since the National Institute of Oceanography is concerned with age determinations, especially in studies of the life cycle and populations of whales, Dr. Mackintosh and Dr. Laws had made arrangements, after the publication of the paper by Purves (1955) for the collection of a large number of ear plugs from whales taken by factory ships in the Antarctic season of 1955–56. The plugs were obtained from some 454 whales, together with relevant data on the whales from which they were taken. Before examining the material themselves however, they were good enough to make the collection available to us so that the relation between the laminations of the plug and the age of the whales could be further examined. This is the subject of the greater part of the present paper. It was a matter of much interest however, to examine the age composition of the population from which the plugs were obtained and by agreement with the National Institute of Oceanography the paper has been extended beyond its initial scope to include this aspect.

MATERIAL AND METHOD

The ear plugs had been wrapped singly or in pairs and preserved in 5% formaldehyde on board the factory ships and were consequently hard and in good condition for examination in the laboratory. It is unfortunate that a number of plugs had become detached from their wrappings during transit as a result of which it has been impossible to determine the length and sex of the animals involved, but even these specimens have been useful in plotting the age frequency distribution.

Because of the asymmetry and extreme attenuation of the distal end of the core it was thought that bisection of the plug would result in loss or damage to the earliest formed part of the structure, so each specimen was carefully group down to the central plane by hand. The grinding was carried out by rubbing the plug with a rotary movement against waterproof abrasive cloth which had been cemented with rubber solution to a sheet of plate glass. Coarse and fine grades of abrasive were used and during the whole operation a stream of water was directed over the surface of the plate. It is appreciated that for routine examination of the plugs a mechanical grinding plate or stone would be preferable, but since the time expended on each plug using the more primitive method amounted to no more than three minutes, the above described apparatus was considered adequate for the present sample.

Plate 5 shows a series of ear plugs from female Fin Whales, the specimens being chosen at random from groups of plugs which differed consecutively in lamination number by four laminations. The series shows a progressive lengthening of the core of the plug and a gradual darkening of its matrix from the external shell towards the central axis. From the plate it appears that the overall length of the core of the plug is no guide to the number of laminations which it contains, but it will be shown later that in spite of the great variability in the lengths of the cores of equal laminar number, the average length of the core per lamination number is correlated with the number of laminations. It may be stated that on the whole, the diminution in the thickness of the laminations from the distal to the proximal end of the core is more regular in plugs from males than in those from females. This characteristic is not always apparent in a small sample, and cannot be used as a guide to the sex of a whale from which any one plug originated but may be of use statistically in connection with a large sample of specimens. The unwrapped specimens referred to on page 161 were divided on the basis of this feature but the information so obtained has been of limited use and is referred to with reservation in the present paper.

In the plugs from immature and very young animals the primary laminations may be subdivided into a number of ill-defined, subsidiary layers but the latter become obliterated as more primary laminae are formed and it has been the practice throughout this investigation to treat every lamination in the older specimens as a single unit, however narrow and apparently subsidiary In the very old specimens the proximal end of the core may appear to the naked eye or with dissecting binoculars to be quite undifferentiated, but when examined microscopically, these undifferentiated areas are seen to be made up of a series of regularly-spaced refractive layers. When these layers are counted towards the distal end of the core they are observed to increase gradually in thickness and in the latter respect to be in geometrically progressive sequence with the coarser layers which are visible to the naked eye. The microscopic section shown in Plate 6 was taken from the proximal end of the only plug in which for some unknown reason there was a sharp transition from very coarse to very fine laminae, but it is useful in that a comparison can be made between the two types of laminae within the compass of a very small section. The section shows the appearance of the refractive layers referred to above after removal of the ceruminous component. The area bottom left, which shows the lateral extremity of the short axis of the base of the core originally contained very little cerumen and consists of a mass of undifferentiated squamae of keratin. On the right, the squamae are broken into a series of laminae of approximately equal thickness, each of which contains a number of flattened nuclei.

The upper part of the section shows two of the very coarse laminae. When stained with haemalum and Mallory's triple stain the greater part of the keratinized mass appeared bright blue, but in each lamina there was a conspicuous band of orange which occupied a position immediately distal to the layer of flattened nuclei. These bands of orange, which are deemed to mark areas of imperfectly keratinized cellular matter accompanying degenerate nuclei, seem to be the main distinguishing feature of the laminations and each can be used as a criterion of what is a single lamination. If it were possible to cut and stain the whole core in this manner the lamination number could be estimated with great accuracy. In the more simple method of counting the laminations on the unstained cut surface of the core it would be improbable to make an error of more than plus or minus 4 laminae in each plug and with a large sample, such as the one under consideration, errors of this magnitude would probably cancel each other out.

All the specimens referred to in this paper were collected aboard the factory ships *Baleana*, *Southern Harvester* and *Southern Venturer*. The *Southern Harvester* collection was obtained from that sector of the Antarctic known as the " Sanctuary " (Lat. 60° W.–120° W.) and is referred to as the Area I sample. The *Balaena* collection was obtained from Area II whilst the *Southern Venturer* collection was obtained from both sectors. The latter collection has been broken up and amalgamated with the *Balaena* and *Southern Harvester* specimens so that only the two populations, the Area I and Area II samples are described.

The data referred to in the text are given in Tables A to D of the Appendix.

From the results of the examination of the Steinsham material (*loc. cit.*) it has been established that there is a direct correlation between the number of laminations in the core of the plug and the age of the animal as assessed from the ridges on the baleen plates. This correlation can however be shown only in respect of animals under 6 years of age, since the analysis of the baleen plate data becomes difficult after this age.

Before attempting to obtain the age frequency distribution it is necessary to establish whether or not this age lamination correlation continues throughout life. It may reasonably be assumed that the growth of cetaceans follows a pattern similar to that which is found in most other mammals and that there is an age shortly after sexual maturity beyond which further increases in bodily proportions are small relative to the immature growth increments. This being so, one might expect a certain variability in the adult dimensions due to the differential immature growth rates. If a simple relationship can be shown between the skull width and the lamination number as suggested by Purves (1955) then the lamination number would be valueless as a means of estimating the individual ages of a variable adult population the individual growth rates of which are unknown.

Unfortunately no data relevant to skull width are available for the present sample so that the skull-width-lamination number relationship cannot be found directly. Mackintosh & Wheeler (1929) have published a very comprehensive list of skull widths and body lengths of Fin Whales so we may use their figures relevant to the range of lengths available in the present sample to find the body-length skull-width relationship.

The Body Length, Skull-width Relationship

In the Tables of the External Characters of Fin Whales, Mackintosh & Wheeler (1929) quote the skull widths and total lengths of 162 female and 206 male Fin Whales taken at South Georgia during the years 1926 and 1927. The hypothesis

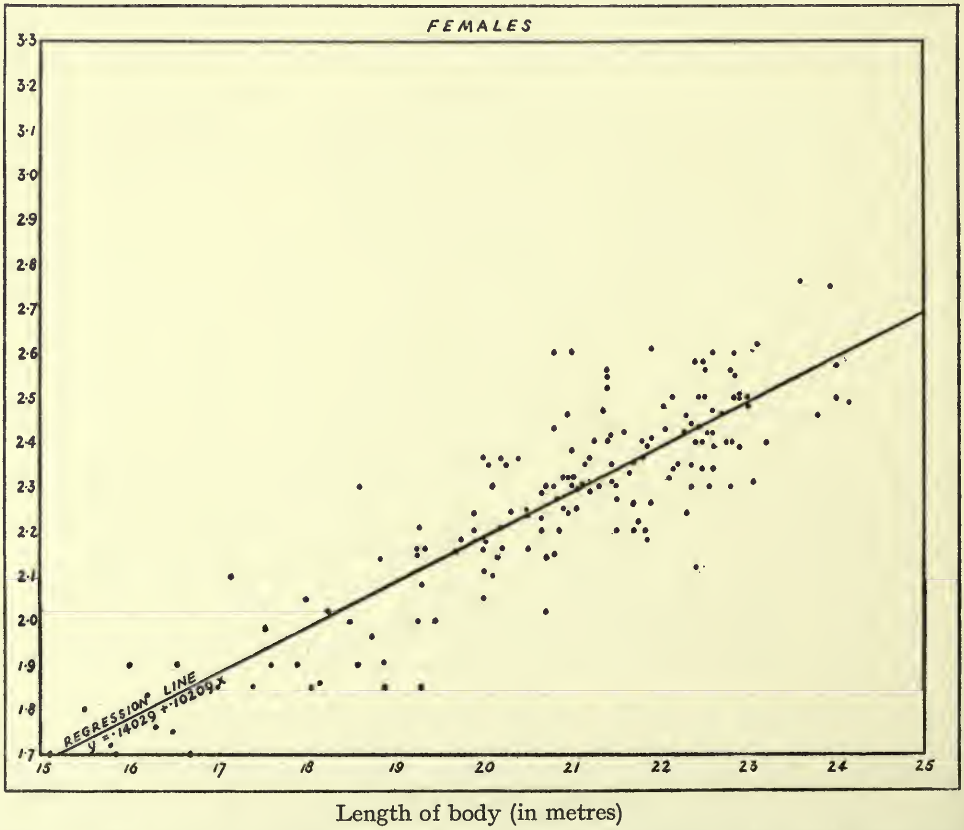
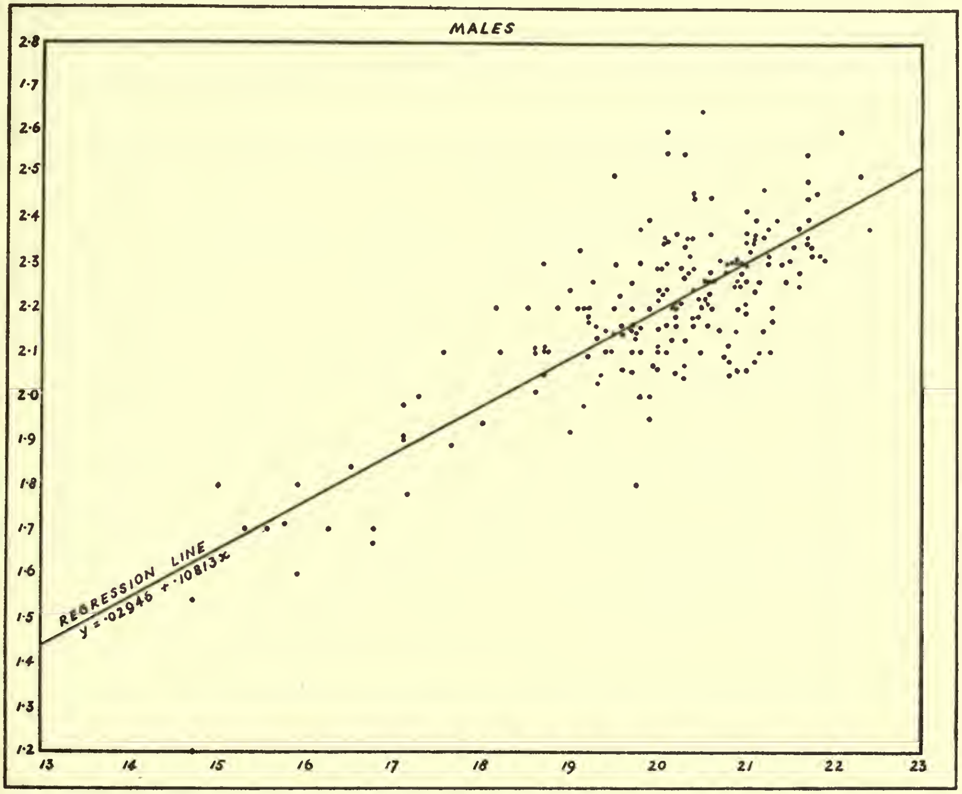


Fig. 1. The skull width-body length relationship of a population of female Fin Whales *Balaenoptera physalus* measured at South Georgia, Mackintosh & Wheeler (1926–27).

of a linear relationship between the skull-width and total length provides an excellent fit to the data. The linear regression of skull width on total length (Text-figs. 1 and 2) is found to be :

$y = 0{\cdot}14029 + 0{\cdot}10209x$ for females (Text-fig. 1) and $y = 0{\cdot}02946 + 0{\cdot}10813x$ for males (Text-fig. 2) where y and x are the skull width and total length in metres



Length of body (in metres)

FIG. 2. The skull width-body length relationship of a population of male Fin Whales *Balaenoptera physalus* measured at South Georgia, Mackintosh & Wheeler (1926–27).

respectively. It must be emphasized that the linear relationship is only valid in the above range. It is of incidental interest to note that the rates of increase of skull width on total length for female and male whales are not significantly different.

A measure of the high degree to which the association between skull width and total length approaches a linear relationship is given by the correlation coefficient which is as great as 0·87 for the females and 0·80 for the males. There is thus no justification for rejecting the hypothesis of an isometric relationship between the skull width and total length of the Mackintosh & Wheeler population. It is a justifiable inference to conclude that this isometric relationship holds for all populations of this species in which the total lengths lie in the range 14 metres to 24·3 metres. In particular it holds for populations in Areas I and II. It is therefore possible to deduce the lamination-number skull-width relationship from that holding between the lamination number and total length.

It is of some bearing on the above topic to compare the Mackintosh & Wheeler sample with the Area I sample for their common measurement of total length. The former population is truncated of several extreme small values so that the bottom limit for each sex in the two samples is the same. It has been necessary for ease of comparison to convert Mackintosh & Wheeler's small 1-metre length ranges to the mean value in feet. The figures are given below:

Male Fin Whale S. Georgia		Female Fin Whales S. Georgia	
Length	Number of measurements	Length	Number of measurements
55	6	—	—
58	7	58	6
61	13	61	11
64	45	64	9
67	78	67	30
70	45	70	36
73	3	73	38
77	1	77	8
80	—	80	1

The length frequency distribution of the specimens from Area I is given below:

Male Fin Whales Area I		Female Fin Whales Area I	
Length	Number of specimens	Length	Number of specimens
55	3	—	—
58	3	58	5
61	12	61	12
64	49	64	17
67	76	67	30
70	26	70	60
73	2	73	30
77	0	77	7
80	—	80	1

Inspection of the above lists of measurements shows that the length frequencies of both samples are arranged more or less symmetrically about the mean lengths. The mean lengths and standard deviation for the two samples were found to be:

		Mean length	Standard deviation
S. Georgia	Males	66·0	3·6
Area I	,,	66·0	3·1
S. Georgia	Females	68·7	4·6
Area I	,,	68·6	3·3

It is obvious that the two samples are remarkably alike in their distribution of the total lengths. On the other hand the 38 female and 23 male specimens caught in Area II give the following value :

		Mean length	Standard deviation
Area II	Females	70·1	4·5
Area II	Males	67·0	3·7

Although as shown by a " *t* test " the differences in mean total length between the Area II and the Area I whales are not significant at the 95% level there is some slight evidence for suspecting that the mean total lengths of both sexes in Area II are approximately 1 ft. greater than those in the Area I sample. The values of mean total length given above are only valid over the length range 55 ft. to 80 ft. and would be rather lower over the whole length range of the population.

The Lamination Number–Body-length Relationship

In Text-figs. 3 and 4 the lengths of males and females from Areas I and II respectively have been plotted against the lamination number. Certain facts which will be examined in detail are given below :

(*a*) There is considerable variation in length at every lamination number.

(*b*) At every lamination number the average length of the females is greater than that of the males.

(*c*) The average length per lamination number of the specimens from Area II is greater than that of the specimens from Area I.

(*d*) After the formation of the eighth lamination the number of individuals in each laminar group is inversely related to the number of laminations.

The mean body length for each lamination group is given in the following tables :

Sample Area I

	Female Fin Whales		Male Fin Whales	
Lamination number	Number of specimens	Mean length in ft.	Number of specimens	Mean length in ft.
3½	—	—	1	55
4	—	—	2	69
5	1	58	—	—
6	4	65·75	1	64
7	8	64	2	58
8	6	61	2	64
9	11	64	8	63·4
10	9	65	5	63·4
11	6	65	3	63
12	8	67·7	5	64
13	3	67	8	66
14	7	69	9	65·3
15	3	70	5	66
16	8	72	9	66
17	3	71	7	67
18	4	71	1	69

Sample Area I—cont.

Lamination number	Female Fin Whales		Male Fin Whales	
	Number of specimens	Mean length in ft.	Number of specimens	Mean length in ft.
19	1	74	2	66
20	5	71	5	66
21	1	74	2	70
22	4	71	5	68
23	1	73	7	67
24	8	72	5	67
25	2	71	3	66·6
26	6	72	3	67
27	3	72	2	65
28	2	71	3	66·3
29	2	68·5	2	69
30	1	73	4	66·5
31	1	70	2	66·5
32	5	74	1	65
33	1	75	1	70
34	2	—	1	71
35	1	75	4	66
36	6	72	1	68·5
37	1	76	1	65
38	—	—	1	67
39	1	73	1	69
40	5	71	2	68·5
41	—	—	—	—
42	2	73	1	66
43	1	69	3	66·5
44	—	—	2	66
45	1	72	1	68
46	1	75	2	67
49	—	—	1	67
50	2	75	3	67
52	—	—	2	66
53	—	—	1	65
54	2	76	3	66
55	1	69	1	66
56	3	71	2	64
58	—	—	2	66·5
59	—	—	1	67
60	—	—	2	69
61	—	—	1	68
62	—	—	1	73
63	—	—	1	70
66	—	—	1	65
67	—	—	1	70
70	1	75	1	71
71	—	—	1	65
75	—	—	1	68
76	—	—	2	66·5
80	1	73	—	—
83	—	—	1	64
85	—	—	1	64

Sample Area II

Lamination number	Female Fin Whales		Male Fin Whales	
	Number of specimens	Mean length in ft.	Number of specimens	Mean length in ft.
3	1	60	—	—
4	—	—	—	—
5	2	64·5	1	55
6	1	63	—	—
7	3	61	—	—
8	1	74	2	63
9	3	65·5	4	64
10	3	67	1	63
11	3	72	1	66
12	5	70·6	—	—
13	1	72·0	—	—
14	1	72	1	65
15	1	72	—	—
16	1	68	2	69·5
17	—	—	1	68
18	1	76	—	—
19	1	76	1	71
20	1	72	2	71
21	3	73·6	—	—
22	2	72·5	1	70
23	—	—	2	69
24	1	75	—	—
28	1	73	—	—
29	1	77	—	—
30	1	75	1	69
31	1	73	1	70
32	3	75	—	72
33	1	75	—	—
34	1	75	2	68
26	—	—	1	70
38	1	68	—	—
40	—	—	2	69
42	1	72	—	—
43	1	75	1	70
44	1	78	1	71
45	—	—	1	67
46	1	77	—	—
47	1	74	—	—
48	1	76	—	—
50	1	74	1	67
52	1	75	—	—
53	1	79	—	—
59	—	—	1	65
62	1	75	—	—
63	—	—	1	76
66	1	78	—	—
76	—	—	—	63

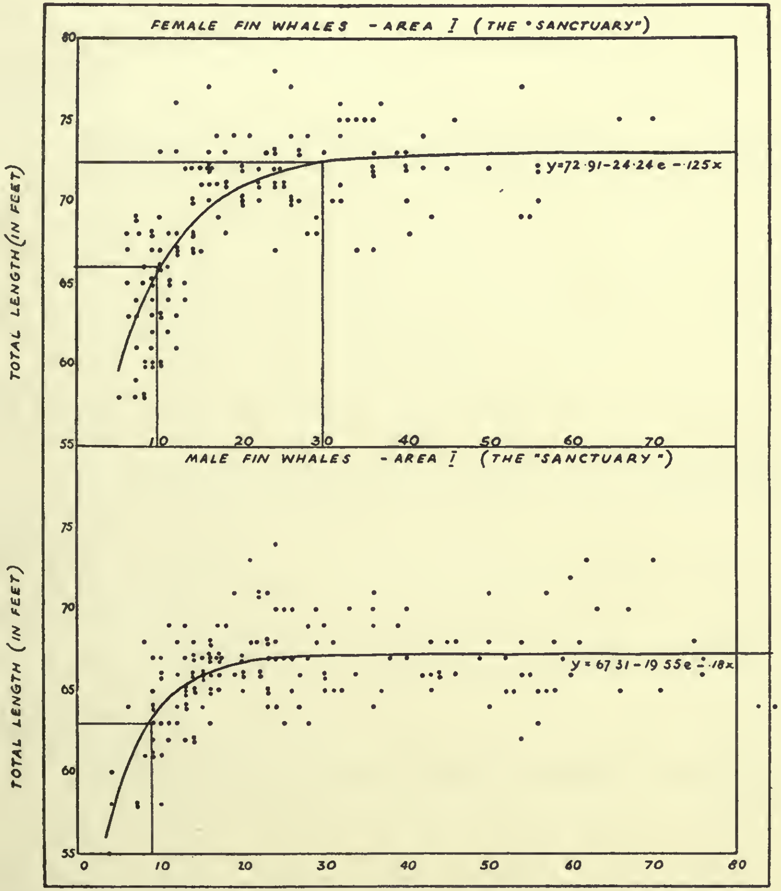


FIG. 3. The ear-plug lamination number—body length relationship of a population of Antarctic Fin Whales *Balaenoptera physalus* captured during 1955–56.

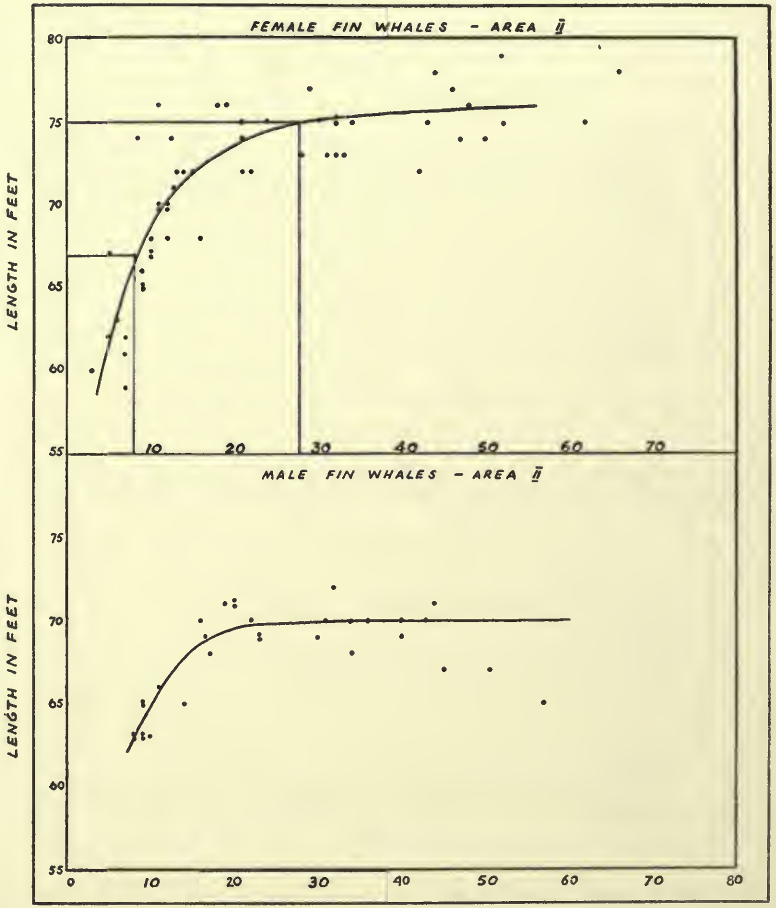


FIG. 4. The ear-plug lamination number—body length relationship of a population of Antarctic Fin Whales *Balaenoptera physalus* captured during 1955–56.

Text-figs. 3 and 4 suggest that for each sex, whales with more than 13 laminations are such that their total lengths are almost independent of their lamination numbers, i.e. the correlation coefficient between lamination number and length is not greatly different from zero for whales with more than 13 laminations in the ear plug. This correlation coefficient was evaluated as 0·169 for females and 0·27 for males in Area I. Using $t = r\sqrt{\frac{(n-2)}{(1-r^2)}}$ as a t-variate where "r" and "n" are the correlation coefficient and the number of individuals in the sample respectively, both of the above coefficients were found to be not significantly different from zero. This same analysis applied to the Area II whales revealed that as in Area I the lamination number was nearly independent of total length for whales with more than 13 laminations, i.e. for any Fin Whale with a lamination number greater than 13 the specific value of its number can be considered to have little bearing on its total length and skull width.

If any one plug is measured from its base to each successive lamination the increase in core length is found to take the form of an exponential curve like that which was described by Purves (1955), but the total length of the core for any one lamination number varies very greatly from one specimen to another, and cannot be used even as a rough guide to the lamination number. An average growth curve has been obtained (Text-fig. 5) by plotting the mean length of the core per lamination number at every fourth lamination against the lamination number. These mean core lengths are remarkably similar in the two sexes notwithstanding the difference of over 4 ft. in the adult body lengths between males and females. The curve appears to show that plugs of high lamination number are disproportionately long, but this effect may be due to the small number of plugs of high lamination number in the sample. If high lamination number is an indication of old age the presence of these disproportionately long plugs may be due to the mixing of populations owing to lateral migration Brown (1954). It will be seen at once that this growth curve is in no way comparable with that of skull width against body length so that neither the lamination number nor the plug length have any close relationship to the body length and skull width. It must, therefore, be concluded that the growth of the plug is independent of that of the body as a whole, and that its laminated core forms part of a rhythmic growth system which was initially established in response to one or more of a number of factors involving the passage of time, such as the breeding cycle, migratory movements, nutritional changes, temperature variation or inherent mammalian moulting cycles. The periodicity of the rhythm may vary from one individual to another but in a population with a very regular cycle of behaviour the variation is likely to be very small. Since the growth of the plug is not conditioned by the skull dimensions, it is possible that the shape of the bony meatus is continually adjusted to the growth increments, that there is no resorption of any part of the plug, and that the laminations constitute a complete record of the periodic desquamations from birth to death. In this connection it is of interest to draw attention to the difference between the growth of the ear plug in whales and that of the cycloid and ctenoid scales of fishes. Van Oosten (1955) states that in the fishes cessation of body growth ultimately ends in suspensions of scale formation. He continues

" In maintaining coverage of the body the scales have been found to grow at an approximately fixed ratio with the fish. The growth of the scale, is therefore, more or less a replica of that of the body. This fact has made possible the employment of scales in estimating the past growth of an individual. Multiplying the ratio of the length of that part of the scale that was completed at the end of a certain year of life to the final length of the scale by the length of the fish gives the estimated length

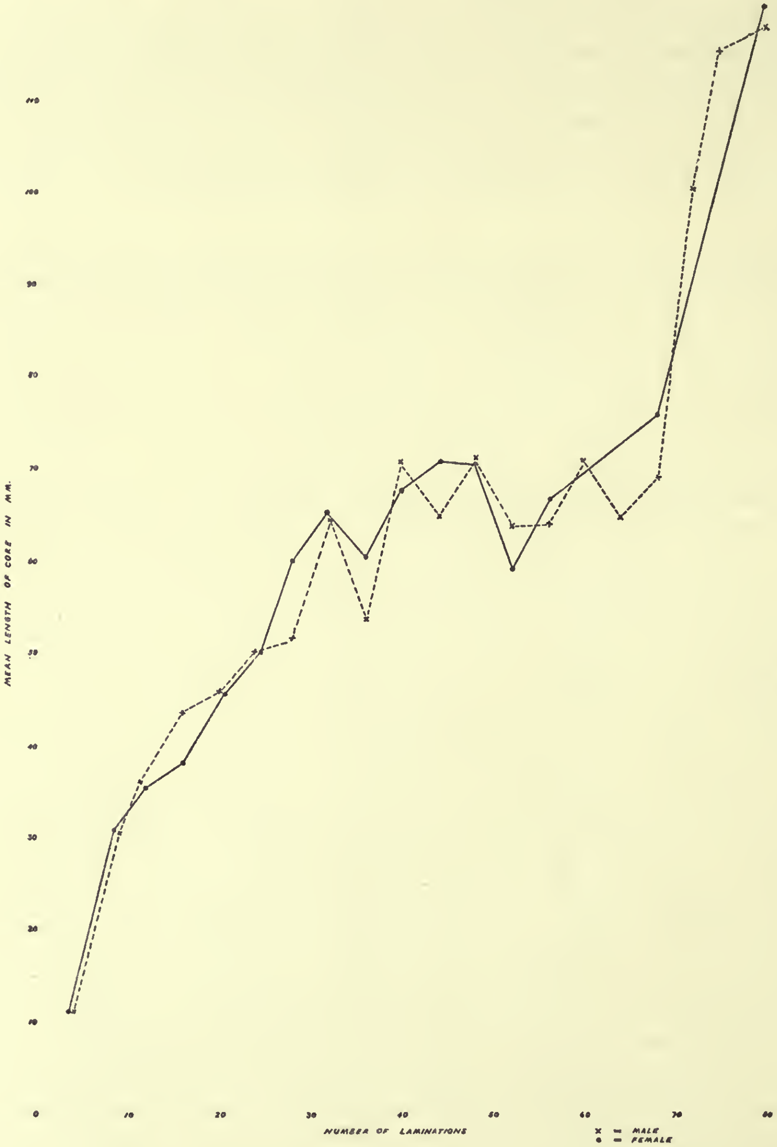


FIG. 5. Lamination number-core length relationship of the ear-plugs of a sample of Fin whales *Balaenoptera physalus*.

that the individual attained at that particular age. Yearly increments of growth can be obtained by subtracting the different computed lengths ". A similar system of length estimation based on the thickness of ear plug laminae could be arrived at with some difficulty in respect of whales under 6 years of age, but for animals above this age no correlation is possible. Van Oosten also states that age determination in fishes permits studies on variation in growth rate with species, latitudes and different bodies of water. " By observing the time of formation of laminae the length of growing seasons may be determined." It is very doubtful whether environmental conditions have any direct influence on the time of formation of the laminae of the ear plug in whales, although nutritional conditions may to some extent determine their thickness. Since there is strong evidence that lamina formation is an inherent moulting cycle it is very probable that it takes place whether the whale migrates or not. If the rate of moulting can be established the ear plug would probably be a more accurate age indicator than the fish scale.

Since it was shown by Laws & Purves (1956) that up to the formation of the 12th lamination a fairly close correlation exists between body length and lamination number and in the present paper that after the 13th lamination the correlation coefficient approaches, but is not precisely, zero, it might be expected that an exponential growth function could be demonstrated over the whole range of laminations.

In Text-fig. 3 curves of mean total length against lamination number have been fitted by the method of least squares to the samples of males and females from Area I. Dealing first with Area I females it was found that if " y " (in feet) is the length and " x " is the lamination number then a good fit to the data is given by

$$y = 72{\cdot}91 - 24{\cdot}24 \ \exp \ (-0{\cdot}125x)$$

where " exp " is the exponential function. This expression is a description of the data only over the lamination range 6–80 and gives a growth curve from 61·5 ft. at 6 laminations to a maximum length of 72·91 ft.; extrapolation beyond these limits is not justified but Mackintosh & Wheelers' (1929) curve of immature body lengths can be used to complete the curve.[1] It may be noted that a length of 71·9 ft. is attained at the formation of the 26th lamination. The line in the graph (Text-fig. 3) represents the growth function, which is such that at any given lamination number the growth rate is proportional to the " remaining size " i.e., the maximum size minus the size reached. A similar growth curve was fitted to the males Area I (Text-fig. 3) and a good fit was obtained by the curve

$$y = 67{\cdot}31 - 19{\cdot}55 \exp (-0{\cdot}18x).$$

Here again the curve only describes the growth in the range 6–80 laminations. The estimated length of 60·7 ft. at 6 laminations increases to an average maximum of 67·31 ft. The length of 66·3 ft., one foot less than the maximum is achieved at about the 16th lamination. The points marked on the 2 diagrams are the mean values of the lengths for each lamination number. This result is in accordance with previously established information regarding the difference in the growth rates between male and female Fin Whales and both curves approximate to the average mammalian growth curve. It will, therefore, be assumed that the laminations are laid down at fairly regular intervals throughout the life of the animal.

---

[1] Because of the under-representation in the sample of the 6th lamination group the first part of the growth curve may give an over-estimation of the average body length in this group, see page 149.

The Rate of Formation of Laminae

In order to establish the rate of formation of the laminae, use can be made of the following information :

(*a*) The lowest number of laminae formed when the majority of the females are either lactating or pregnant.

(*b*) The lowest number of laminae formed when the vertebral epiphyses are ankylosed to the centra in the majority of adults.

The difference between these two figures will represent the approximate number of laminae formed between sexual and physical maturity which by deduction from Wheeler's (1929) figure of 15 corpora lutea accumulated in the ovary and Laws' (1955) rate of 1·4 per annum for their accumulation should be approximately 10 years.

In Text-figs. 6 and 7 each horizontal line represents the vertebral column and can be considered to be divided into four sections containing the anterior thoracic, posterior thoracic, lumbar and caudal vertebrae respectively. Each vertebral column or portion of a vertebral column has been placed in one or more of the vertical divisions according to the state of fusion of the vertebrae. A category described as " Fused Joint Visible " was given in the original data but for the purpose of the charts it was assumed that if the joint was visible it must also contain a thin layer of cartilage, so vertebrae in this category were placed in the division labelled " Unfused Fine Cartilage ". The horizontal lines in Text-fig. 6 have been thickened to denote whales which were known from the data to be pregnant.

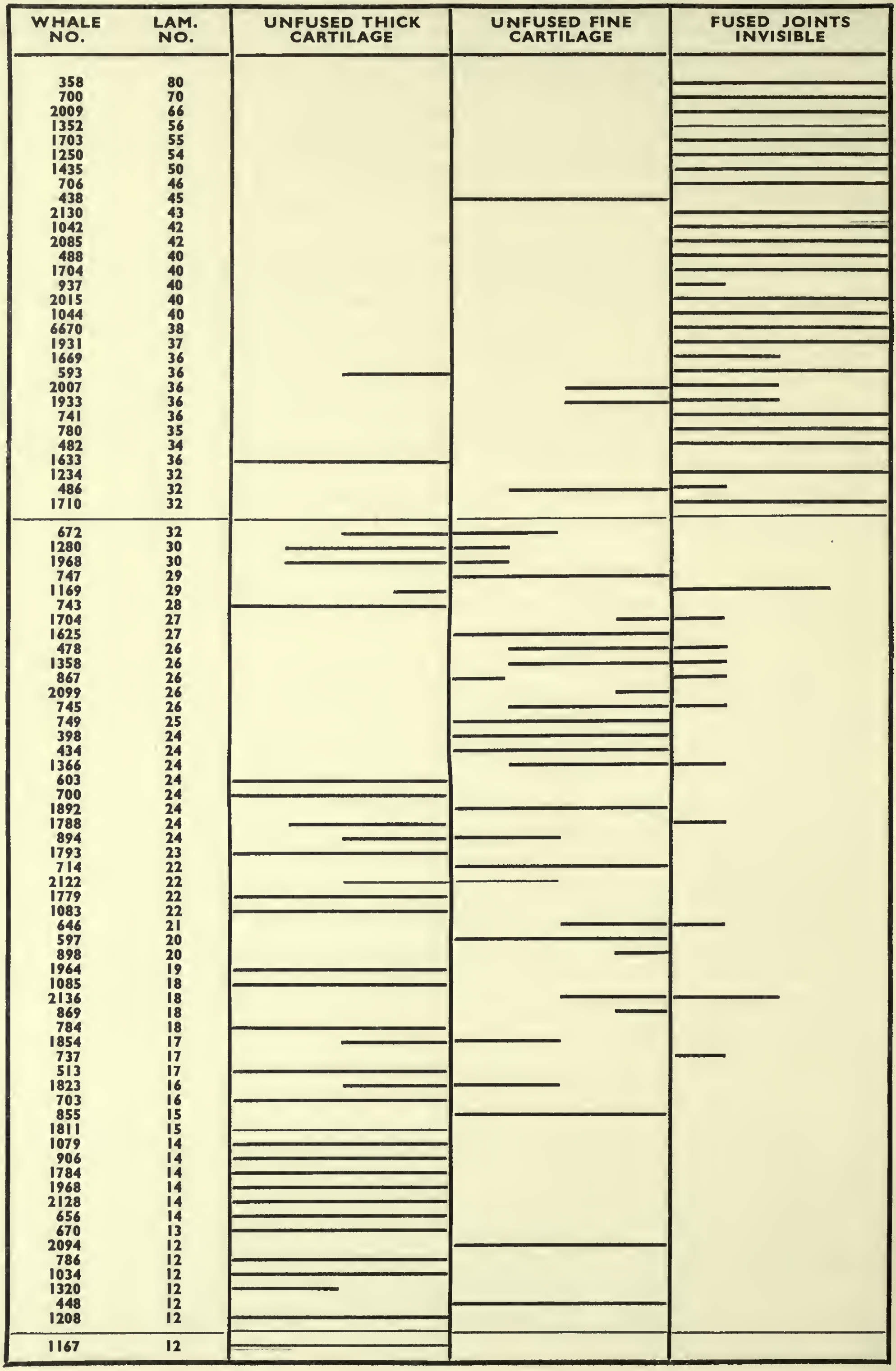
The horizontal lines which completely traverse the charts are drawn through the lamination numbers above which the vertebral epiphyses are fused and invisible in the majority of individuals, and through the number in the chart of the female whales above which the majority are pregnant. It will be seen from Text-fig. 6 that the number of laminations shown between these two lines is 20 so that if the estimated period between sexual and physical maturity is 10 years the rate of lamination formation is approximately 2 per year.

As a check on the above result it may be noted that Mackintosh & Wheeler's figure for the length of female Fin Whales at sexual maturity is 66 ft. This figure has been confirmed by Peters (1939), Mackintosh (1942), Brinkmann (1948), Nishiwaki & Hayashy (1950), the length at physical maturity being in the region of 72·4 ft. The regression line of growth (Text-fig. 3) passes through these two lengths at the 10th and 30th lamination respectively. If the period between sexual and physical maturity is 10 years the rate of accumulation of laminae is 2 per year. When the figures of Nishiwaki & Oye (1951) and Jonsgård (1952) of 67 ft. at sexual maturity and 75 ft. at physical maturity are applied to the growth curve of the Area II females (Text-fig. 4) they are seen to cut the curve at the 8th and 28th lamination respectively.

Here again if the period between sexual maturity and physical maturity is 10 years then the rate of accumulation of laminae is 2 per year.

Up to date no collection of Blue Whale ear plugs large enough for statistical analysis has been received but from inspection of the few specimens which were collected by Simons (1956) there is no reason to conclude that the rate of accumulation of laminae differs greatly from that estimated in the Fin Whale ear plugs. In this connection a letter received from A. H. Laurie is quoted below :

> " Your query as to the interpretation of the figures given in my paper (Laurie, 1937) has resulted in the unearthing of an error which appears to have lain unnoticed for twenty years. On page 250 I have shown that the annual increment of corpora lutea, now called corpora albicantia, appears to be slightly in excess of one per annum. The average figure given was 1·13.
>
> " As is seen in the tables, the above conclusion is based on samples containing three categories of whale, namely pregnant, resting (i.e. neither pregnant nor having recently ovulated), and non-pregnant but having recently ovulated.
>
> For convenience I reproduce here the totals in this argument :
>
> | Percentage pregnant | | Percentage resting | | Percentage recently ovulated |
> |---|---|---|---|---|
> | 64 | . | 24 | . | 12 |
>
> " Where the mistake arises, and I have repeated it categorically in section 6 of the Summary (p. 268) is that I have taken the annual increment to apply to the whole adult stock of female Blue Whales. At the same time no account has been taken of that fraction of the stock which was lactating, and thereby absent from the sample. To clarify this statement let us add a hypothetical but plausible number to the above percentages, to include the absent lactating whales and let us assume that the number of lactating whales corresponds to a similar percentage of pregnant whales in the previous year. The total stock is then represented by 100 (as above) plus an additional 64.
>
> " The total is thus 164, of which the additional 64 just added, being in lactation can be presumed not to have ovulated during the year under review. It follows therefore that the figure given for annual increment of corpora albicantia must be corrected thus :
>
> $$1{\cdot}13 \times \frac{100}{164} = 0{\cdot}69.$$
>
> " Another way of stating the amendment is to say what I should have said in the first place, namely that the average increment in corpora lutea per *breeding cycle* is 1·13.
>
> " If we now employ the revised figure of 0·69 c.l. per annum for Blue females as a whole, the putative time scale can be revised as follows.
>
> " Physical maturity was shown to coincide with the accumulation of 11 corpora. After allowing 1·91 corpora for the first breeding season, i.e. to include



WHALE NO.	LAM. NO.
358	80
700	70
2009	66
1352	56
1703	55
1250	54
1435	50
706	46
438	45
2130	43
1042	42
2085	42
488	40
1704	40
937	40
2015	40
1044	40
6670	38
1931	37
1669	36
593	36
2007	36
1933	36
741	36
780	35
482	34
1633	36
1234	32
486	32
1710	32
672	32
1280	30
1968	30
747	29
1169	29
743	28
1704	27
1625	27
478	26
1358	26
867	26
2099	26
745	26
749	25
398	24
434	24
1366	24
603	24
700	24
1892	24
1788	24
894	24
1793	23
714	22
2122	22
1779	22
1083	22
646	21
597	20
898	20
1964	19
1085	18
2136	18
869	18
784	18
1854	17
737	17
513	17
1823	16
703	16
855	15
1811	15
1079	14
906	14
1784	14
1968	14
2128	14
656	14
670	13
2094	12
786	12
1034	12
1320	12
448	12
1208	12
1167	12

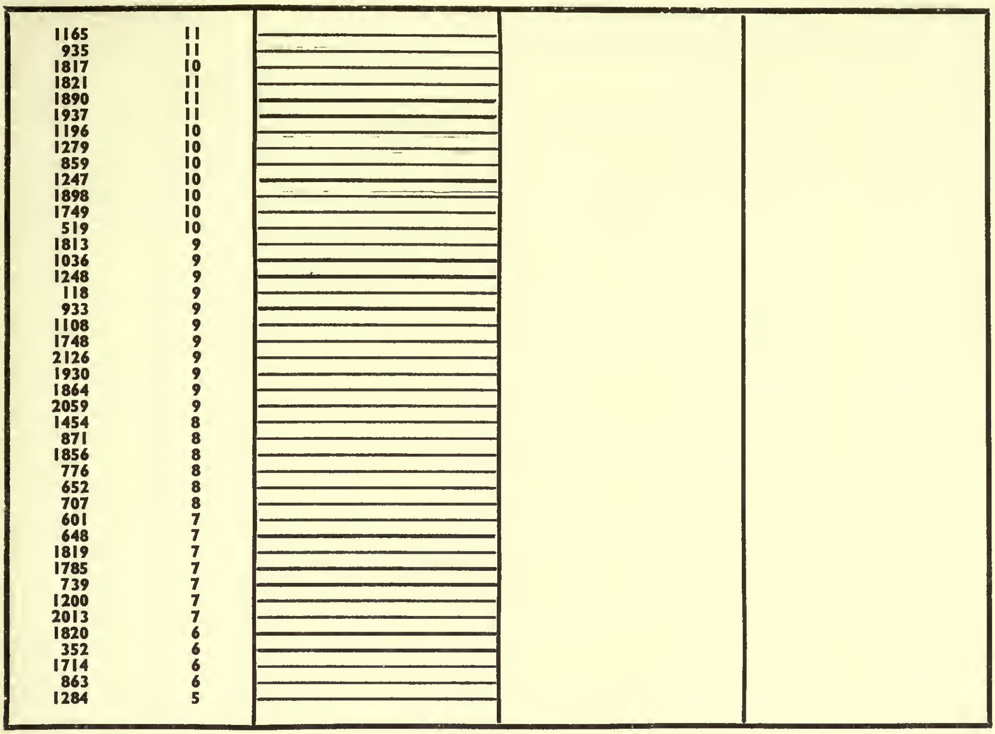
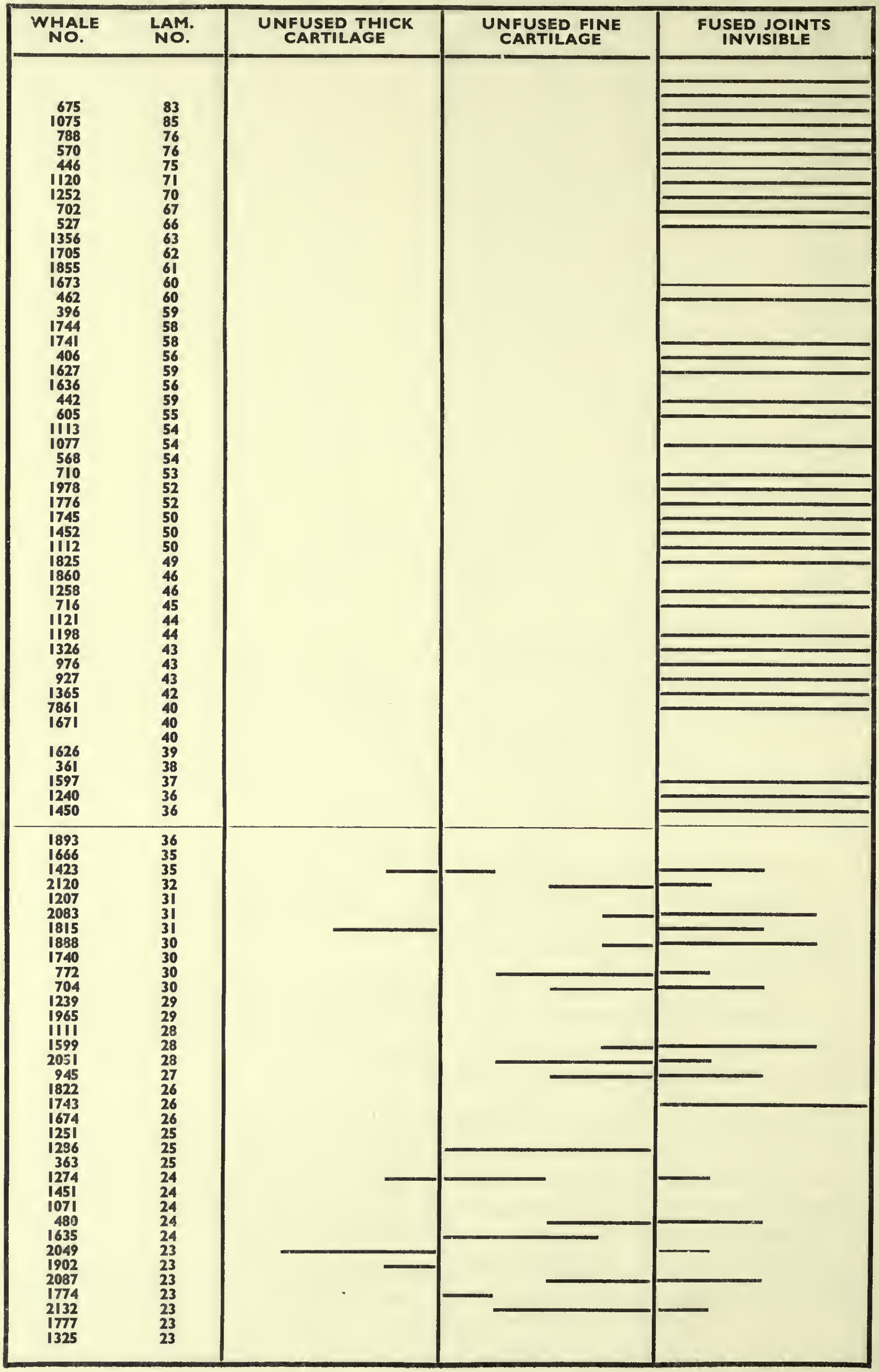


FIG. 6. State of fusion of the vertebral epiphyses of a sample of female antarctic Fin whales *Balaenoptera physalus*. Each horizontal line represents a vertebral column which can be considered to be divided thns AT PT L C where AT = anterior thoracic PT = posterior thoracic, L = lumbar, C = caudal. The thick lines represent individuals which were known to be pregnant.

> a period of 2½ years from birth, the remaining 9·1 corpora could represent 13·2 years so that the age at physical maturity now becomes 2·5 + 13·2 = 15·7 years, instead of 10 to 11 years. The oldest whale in my collection was approximately 45 instead of 30.
>
> " I must emphasise that the above figures relate to the ' ovary clock ' of more than twenty years ago. In view of the much higher percentage of pregnancy now observed in whale samples, the regulator of the clock has apparently been altered, presumably by external influences."

It will be noted that the age at physical maturity for Fin Whales was assessed at 15 years and that the oldest specimen recorded in the present sample was 42½ years old. From the ear plug and ovary data therefore, both Fin and Blue Whales appear to become physically mature at the same age and it may be presumed that they have much the same maximum life span.

Regarding the male Fin Whales the evidence is rather less conclusive. According to Jonsgård (1952) " the various investigations show that these attain sexual maturity



WHALE NO.	LAM. NO.	UNFUSED THICK CARTILAGE	UNFUSED FINE CARTILAGE	FUSED JOINTS INVISIBLE
675	83			
1075	85			
788	76			
570	76			
446	75			
1120	71			
1252	70			
702	67			
527	66			
1356	63			
1705	62			
1855	61			
1673	60			
462	60			
396	59			
1744	58			
1741	58			
406	56			
1627	59			
1636	56			
442	59			
605	55			
1113	54			
1077	54			
568	54			
710	53			
1978	52			
1776	52			
1745	50			
1452	50			
1112	50			
1825	49			
1860	46			
1258	46			
716	45			
1121	44			
1198	44			
1326	43			
976	43			
927	43			
1365	42			
7861	40			
1671	40			
	40			
1626	39			
361	38			
1597	37			
1240	36			
1450	36			
1893	36			
1666	35			
1423	35			
2120	32			
1207	31			
2083	31			
1815	31			
1888	30			
1740	30			
772	30			
704	30			
1239	29			
1965	29			
1111	28			
1599	28			
2051	28			
945	27			
1822	26			
1743	26			
1674	26			
1251	25			
1286	25			
363	25			
1274	24			
1451	24			
1071	24			
480	24			
1635	24			
2049	23			
1902	23			
2087	23			
1774	23			
2132	23			
1777	23			
1325	23			

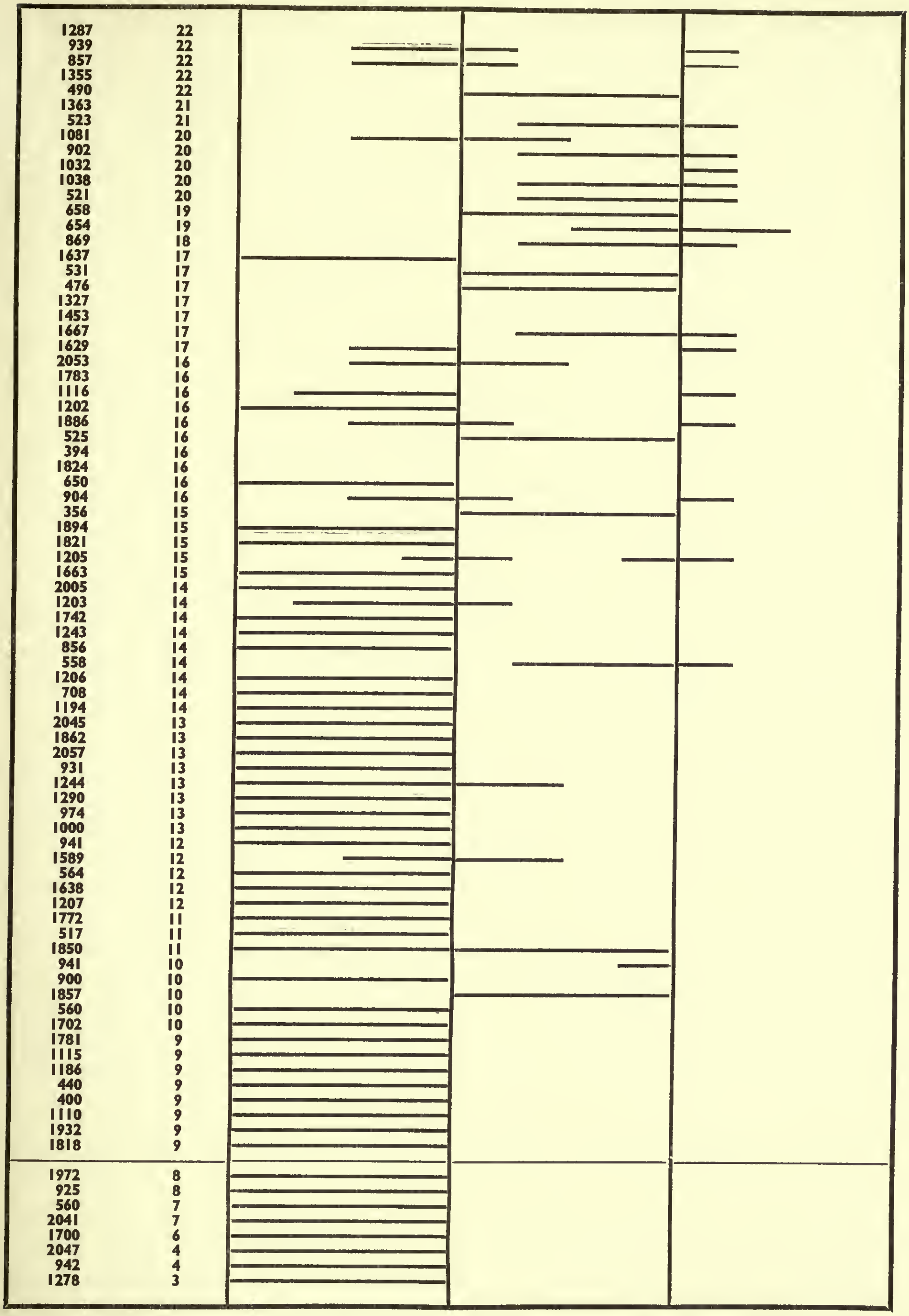


FIG. 7. State of fusion of the vertebral epiphyes of a sample of male antarctic Fin whales *Balaenoptera physalus*. Each horizontal line represents a vertebral column which can be considered to be divided thus AT PT L C where AT = anterior thoracic, PT = posterior thoracic, L = lumbar, C = caudal.

at about 63 ft." The length at physical maturity has been ascertained at approximately 68 ft. by Mackintosh & Wheeler, Peters, Brinkmann, Nishiwaki & Hayashi. In Text-fig. 3 the growth curve of the male whales cuts the 63 ft. ordinate at the 9th lamination, but the upper part of the curve is almost horizontal and covers a wide range of lamination numbers at the average maximum length of 67·31 ft. Referring to the chart (Text-fig. 7) it will be seen that all the vertebral epiphyses are fused after the 36th lamination but as only two individuals are represented in the sample corresponding to the four numbers preceding 36, the actual number formed at physical maturity may be as low as 31. If the rate of laminae formation is approximately 2 per year the male whales would appear to become sexually mature earlier than the females but take longer to become physically mature.

The most recently established data about the ages of sexual maturity are those of Nishiwaki (1952) who quotes 3½ years for males and 4 years for females. The present investigation gives a figure of 4½ years for males and 5–6 years for females. The discrepancy in these two results could be accounted for if the two most distal ear plug laminae could be regarded as being present in the foetus, i.e., the remnant of the epitrichium and the vernix caseosa. Against this hypothesis is the evidence of the ear plug of a 50 ft. long male, collected at Steinsham in 1955. This ear plug had only two laminae, one of which was the "foetal cone" Purves (loc. cit.) and was estimated by Laws & Purves (loc. cit.) to be one year old, and by Ruud, from inspection of the baleen plates to be 1½ years old. The animal was of course much too long to be newly born. According to Sharpey-Schafer (1929) the vesicular cells of the epitrichium are shed late in the intra-uterine life and mingle with the secretion of the sebaceous glands to form a waxy covering, the vernix caseosa. The foetal cone of the ear plug is always very small, undifferentiated, mis-shapen, waxy and in the general appearance could represent the vernix caseosa. The penultimate lamination on the other hand, is always the deepest in the whole series and much too coarse to be present in the foetus. On the basis of the above estimation it represents from 1–1½ years' desquamation during the suckling and first free feeding life of the calf. The discrepancy could also be accounted for if the whales outside the "Sanctuary" become sexually mature earlier than those in Area I.

It may be argued that the ovaries and baleen plates constitute an uncertain guide to the rate of formation of the laminae of the ear plug, so some alternative rates of formation must now be considered. In the first instance it must be stated that the extremely regular appearance of the laminae and the smooth, typically mammalian exponential growth curve afforded by plotting length against lamination number in both sexes of both samples preclude any possibility of a grossly irregular rate of desquamation. It is difficult to conceive of any cyclic phenomenon in the biology of whales or any other mammal for that matter which could account for three moults or desquamations per year. Whales like most other mammals are subject to a bi-annual rhythm of seasonal change and all the accumulated observations on their natural history suggest that their biology and physiology are adjusted accordingly. Any idea of an *average* rate of three desquamations per year derived from an irregular desquamation rate is precluded by the extremely regular appearance of the laminae. If four or more laminations per year are considered than the evidence of the ear plugs collected at Steinsham have some bearing on the problem. In that collection there was one plug (above cited) with only two laminations, one of which was the foetal cone. If the rate of formation of laminae had been four per year then that animal had grown from 21 ft. to 50 ft. in six months, and yet should theoretically have just been weaned at the time of capture. Now the length at weaning, of the Antarctic Fin Whale has been established by Mackintosh & Wheeler (1929) at 39 ft. and since the North Atlantic Fin Whale is known to be smaller than the Antarctic form the average length at weaning of the former is likely to be less than 39 ft. A similar argument could be used for four of the Blue Whales represented in the present collection of ear plugs, since they possessed only two laminations and yet all the animals were over 70 ft. in length, i.e. some 20 ft. above the established length at weaning of the Blue Whale.

Any rate of formation of laminae greater than four per year can be discounted on the basis of the above argument and there is left for consideration the idea of the formation of a single lamination per year.

Assuming the formation of one ear plug lamination per year in the present sample, the ages at sexual and physical maturity of the female Fin Whales would be 10–12 years and 30 years respectively and the oldest specimen some 85 years old. These figures are quite inconsistent with any of the previously assessed ages and growth rates of Fin Whales but are comparable with those in Man and require some critical examination. In the first instance it may be stated that the broad distal lamination was estimated to represent the combined weaning and first free feeding period of the animal's life, i.e. a period of approximately one year. The end of this period would correspond with the time of maximum blubber thickness for that year and would be followed by the northerly migration. If the subsequent desquamation of the whole body followed fluctuations in blubber thickness from year to year, the laminations of the ear plug would be formed annually. If, as seems likely, the ear plug is concerned in the conduction of sound from the blind end of the external auditory meatus to the middle ear, a desquamation rate correlated with blubber thickness would seem to be a necessity

Reverting once more to the subject of ovaries—all authors are agreed that the onset of physical maturity corresponds with accumulation of 15–16 corpora lutea albicatia. If Rund's figure of 1·6 corpora lutea per two years be used as the accumulation rate instead of that of Laws then the period between sexual and physical maturity would be 20 years and not 10 as previously estimated. In the absence of any definite proof of the rate of formation of the ear plug laminae, it can only be stated that the evidence shows conclusively that the rate is either one or two per year and that the latter is more consistent with all the previously accumulated knowledge of the natural history of Fin whales.

THE AGE DISTRIBUTION

Having accepted provisionally the validity of the hypothesis that the rate of increase in lamination-number is two per year, it is possible to form an age-frequency sample distribution from the sample frequencies of the lmination numbers. If " c " represents lamination number and, if it is assumed that the $2i^{\text{th}}$ lamination is first recognizable approximately on the i^{th} birthday, e.g. the 14th lamination on the 7th birthday, and the $(2i-1)^{\text{th}}$ lamination approximately at age $(i-\frac{1}{2})$, then it is seen that whales with $2i$ laminations are between the ages of i and $i + \frac{1}{2}$ years and whales with $(2i-1)$ laminations between the ages of $(i-\frac{1}{2})$ and i years. The sum of the two frequencies of lamination- numbers $(2i-1)$ and $2i$ is thus the sample frequency of the one year group of individuals whose nearest birthday is i years. In the case of the females sampled in Area I only the frequencies of lamination-numbers of 9 or more were used in the construction of the age-frequency distribution, it was considered, because of the corresponding smaller average total body lengths, that the smaller lamination numbers were not fully represented in the sample. The age-frequencies of the Area I females are shown in Text-fig. 8.

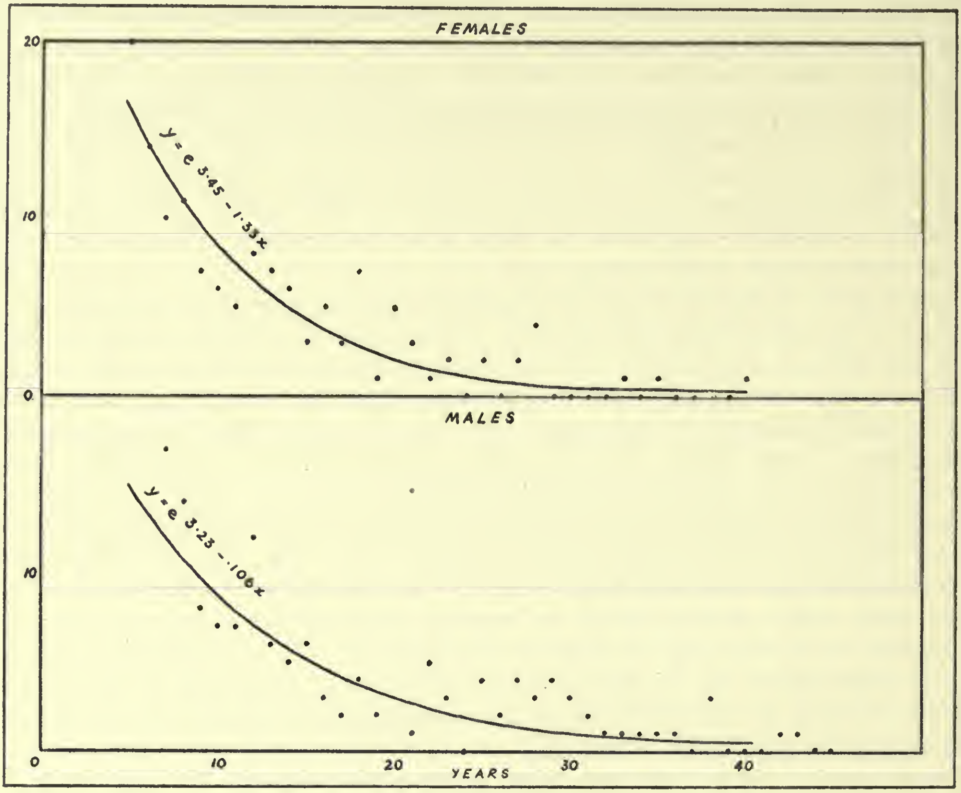


FIG. 8. Smoothed age frequency distribution of a sample of fin whales *Balaenoptera physalus*

At the outset it must be emphasized that owing to the wide variability of the data, the small size of the sample and the possible lack of randomness of selection, due to differences in capture proneness, etc., no more is claimed for the ensuing analysis than that any conclusions based on it are but crude approximations of the true values of the population.

The simplest hypothesis to fit the data is that the mortality rate is constant, i.e. the probability that an individual will survive a further year is independent of its present age. In this case the age frequencies follow a geometrical progression and the points on the graph of the frequency distribution lie on a curve of exponential form. Fitting by weighted least squares, the curve :

$$y = e^{3.45-0.133x}$$

was obtained, where x is the age in years and is seen in Text-fig. 8 to give a fairly good description of the sample frequencies. This curve implies that over the given range of age 5 or more years a proportion $e^{-0.133}$ or approximately 88% of each year group survives to the following year. The insensitive nature of this estimate of survival rate is demonstrated by its 95% confidence interval which ranges from 79% to 97%.

In order to discount the under-representation of the smaller whales the above survival curve was constructed using only the data for not less than 9 laminations at which according to the growth curve in Text-fig. 3 the mean length is 65 ft. The same minimum average length is insured in the sample of males captured in Area I by using only the data of 13 or more laminations. The age-frequencies for the Area I males are shown in Text-fig. 8. As in the case of the females a weighted least squares exponential curve was fitted to the data and as is seen in Text-fig. 8 the curve :

$$y = e^{3.23-0.106x}$$

does reflect the characteristics of the sample frequencies. This curve implies a survival rate of $e^{-0.106}$ or 90% for each year group. There is apparently no evidence of a significant difference in survival rates between the two sexes.

Assuming the perhaps somewhat unreal hypothesis of a stable population, constant in size, it is possible to conjecture estimates of the immature females' mortality rate. The estimation of this mortality rate will be made for each of the following four models of birth rate.

Model 1. First offspring at approximately 5 years old with a succeeding birth rate of one offspring produced every 2 years.

Model 2. First offspring at 6 years old with succeeding birth rate of one offspring every two years.

Model 3. First offspring at 5 years old with succeeding birth rate of one offspring every three years.

Model 4. First offspring at 6 years old with succeeding birth rate of one offspring every three years.

Under the conditions of Model I the expected number of female offspring, assuming that the birthrate is the same for the two sexes, is at the rate of one every 4 years. The total number of female offspring per year is then expected to be approximately :

$$\sum_{i=5} Bl(i) \times \tfrac{1}{4}$$

where $Bl(i)$ equals the number of females in the age group $(i - \frac{1}{2})$ to $(i + \frac{1}{2})$ years old. If B is assumed to be the constant yearly number of female births, then $l(i)$

is seen to be the approximate probability that a female will survive to an age of i years. Equating the two expressions of total yearly female births

$$\sum_{i=5} Bl(i) \times \tfrac{1}{4} = B$$

it follows that

$$\sum_{i=5} l(i) = 4.$$

Now the survival probabilities $l(i)$ are estimated as being proportional to the yearly ordinates of the fitted age distribution curve $y = e^{3.45-0.133x}$
i.e.

$$l(i) = \frac{4\,yi}{\sum_{i=5} yi} \qquad (i > 5)$$

where

$$yi = e^{3.45-0.133i}.$$

The survival probabilities for the other 3 models may similarly be obtained and the numerical values of the $l(i)$ for all 4 models are tabulated in Table I. Thus, for example, it is seen from this table that under the conditions of Model 1 there is

TABLE I.—*Provisional Mortality Rates of Antarctic Fin Whales*

Age i	Observed frequencies	Fitted frequencies	Model 1		Model 2		Model 3		Model 4	
			100 $l(i)$	100 $d(i)$	100 $l(i)$	100 $d(i)$	100 $l(i)$	100 $d(i)$	100 $l(i)$	100 $d(i)$
Under 5	—	—	—	50·0	—	—	—	25·0	—	—
Under 6	—	—	—	—	—	50·0	—	—	—	25·0
5	20	16·130	50·0	6·2	—	—	75·0	9·4	—	—
6	14	14·116	43·8	5·5	50·0	6·2	65·6	8·2	75·0	9·4
7	10	12·353	38·3	4·8	43·8	5·5	57·4	7·1	65·6	8·2
8	11	16·810	33·5	4·2	38·3	4·8	50·3	6·3	57·4	7·1
9	7	9·460	29·3	3·6	33·5	4·2	44·0	5·5	50·3	6·3
10	6	8·279	25·7	3·2	29·3	3·6	38·5	4·8	44·0	5·5
11	5	7·245	22·5	2·8	25·7	3·2	33·7	4·2	38·5	4·8
12	8	6·340	19·7	2·5	22·5	2·8	29·5	3·7	33·7	4·2
13	7	5·548	17·2	2·1	19·7	2·5	25·8	3·2	29·5	3·7
14	6	4·855	15·1	1·9	17·2	2·1	22·6	2·8	25·8	3·2
15	3	4·249	13·2	1·7	15·1	1·9	19·8	2·5	22·6	2·8
16	5	4·718	11·5	1·4	13·2	1·7	17·3	2·1	19·8	2·5
17	3	3·254	10·1	1·3	11·5	1·4	15·1	1·9	17·3	2·1
18	7	2·848	8·8	1·1	10·1	1·3	13·2	1·6	15·1	1·9
19	1	2·492	7·7	0·9	8·8	1·1	11·6	1·5	13·2	1·6
20	6	2·181	6·8	0·8	7·7	0·9	10·1	1·4	11·6	1·5
21–25	7	7·438	4·6	3·6	5·3	3·9	6·9	5·2	8·0	6·0
26–30	6	3·816	2·4	1·5	2·7	1·7	3·5	4·1	4·1	2·5
30–40	3	2·966	0·9	0·9	1·0	1·0	1·4	1·6	1·6	1·6

Note. The above mortality rates were calculated from the age frequency distribution of a single sample of the population using the ear plug lamination as guide to the age. The figures are based on an assumed rate of formation of 2 laminations per year. If the rate of formation is one lamination per year the age increments in column I would have to be doubled.

an estimated proportion of 50% surviving to an age of 5 years and a proportion of 25·7% surviving to an age of 10 years. The value $d(i)$ given in the same table are calculated from the relationship

$$d(i) = l(i) - l(i+1)$$

and therefore 100 $d(i)$ is the estimated percentage of the population which dies between the ages of i and $(i+1)$ years. Thus in Model 1 an estimated 5·5% die between the age of 6 and 7 years. From the columns of $d(i)$ it is seen that the immature mortality rates are such that 50% of the population dies under the age of 5 in Model 1, 50% die under the age of 6 in Model 2, 25% die under the age of 5 in Model 3, and in Model 4, 25% die under the age of 6. It is of some interest to note that if the fitted exponential curve is extra polated backwards to age zero then the ensuing immature death rate is such that 48·7% of the population die under the age of 5 years, and 55% under the age of 6 years, values very close to that obtained under Models 1 and 2.

From the growth curve of Area I females (Text-fig. 3) it is seen that the fitted regression function estimates the mean total lengths at ages 3, 4 and 5 years as 61·5 ft., 64·0 ft. and 66·0 ft. respectively. As the whales prone to capture are restricted to a minimum length of 57 ft., there is a strong likelihood that the given mean values of total length of the 3- and 4-year-olds are over-estimates of the population values at these ages, but as the range of the sample of the 5-year-olds (9 and 10 laminations) is above 60·0 ft. there is no reason to believe that the estimation of this age group has been affected by the size restriction. If the population proportional frequencies of the 3 and 4 years old are assumed to be given by the extrapolated values of the exponential female age-distribution (Text-fig. 8) then as 5 3-year-olds and 14 4-years are present in the sample it may be inferred that approximately 23% of the 3-year-olds and 76% of the 4-year-olds are over 57 ft. in length, and thus prone to capture. As stated before, the sample evidence indicates almost conclusively that 100% of the 5-year-old age group are over 57 ft.

The figure for the percentage of immature whales in the total catch is, of course, dependent upon the age of attaining sexual maturity; this age is assumed to be 4 years in Models 1 and 3, and 5 years in Models 2 and 4. The numbers of females taken in Area I under the ages of 5 and 6 years are respectively 39 and 19 out of a total catch of 156 whales giving the percentage of immatures in the catch as 12·2 for Models 1 and 3 and 25·0 for Models 2 and 4.

CONCLUSIONS

The original hypothesis of a bi-annual rhythm for the formation of the laminae having been supported by correlation with observations on the growth of the baleen plates up to the sixth year of life it remained to establish whether this rhythm continued throughout the life of the animal.

It has been shown that the growth of the plug is not directly associated with the lateral growth of the skull, but that there is an exponential relationship between the total body length and the lamination number.

The exponential growth curve of the body length approximates in form to the

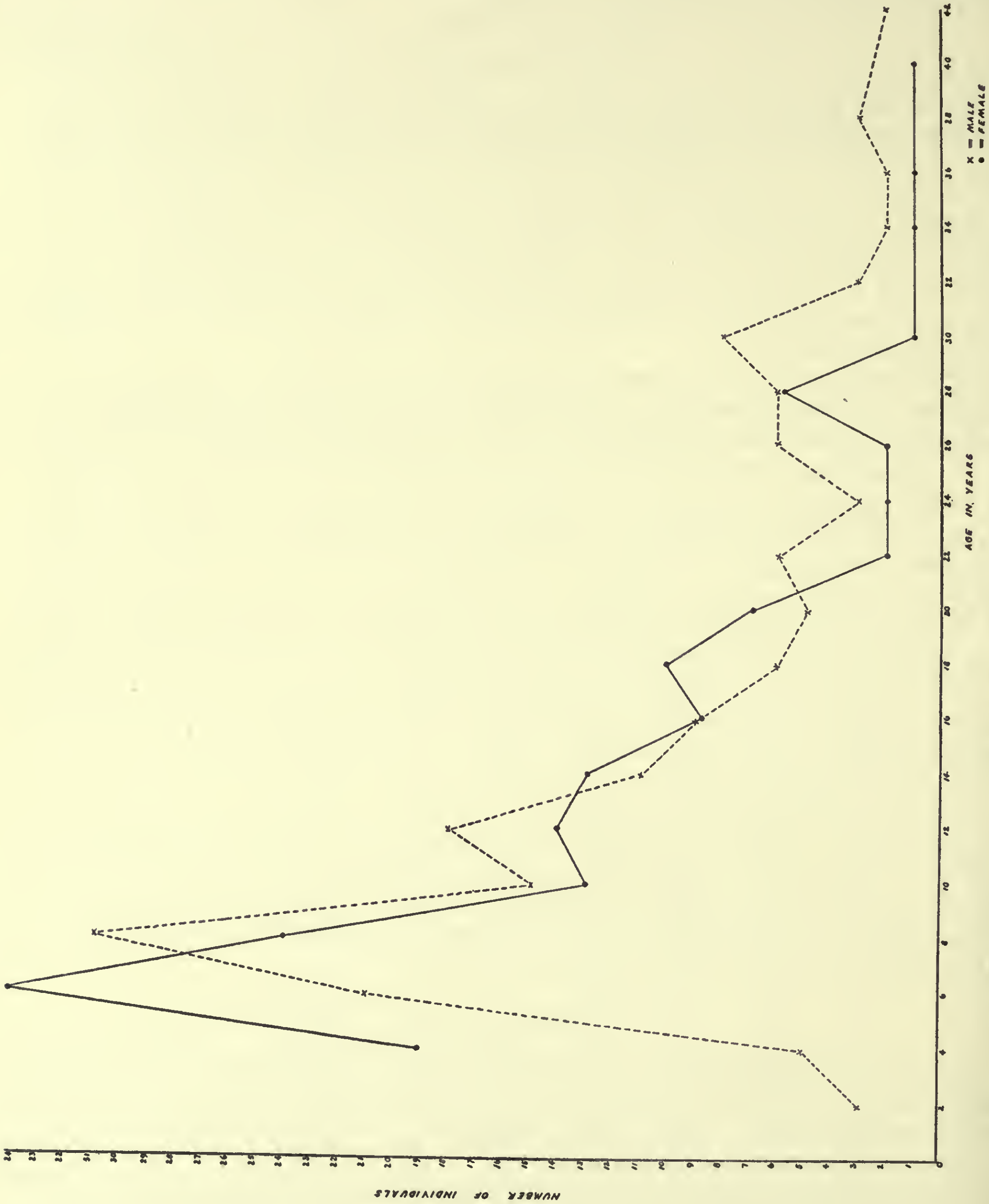


FIG. 9. Age distribution of a sample of male and female antarctic fin whales *Balaenoptera physalus*.

normal mammalian growth curve and it was therefore assumed that the laminae of the ear plug were formed at regular intervals throughout life.

Assuming the interval between sexual and physical maturity to be 10 years as assessed from previously established information about the number and rate of formation of corpora lutea produced during this interval, it has been shown that the rate of formation of laminae is approximately 2 per year.

The previously established total body lengths of female Fin Whales at sexual and physical maturity, i.e., 66 ft. and 72·4 ft. respectively are identical with those deduced from the ear plug body length growth curve using the above rate of laminra formation.

The fact that the average core length per lamination number is almost identical in the two sexes, notwithstanding the difference in the skull proportions, indicates that the method of counting is fairly accurate.

Using the lamination number as a guide to age, the age frequency distribution of the sample takes the form of exponential curves in both sexes. From these exponential curves an age independent adult mortality rate of 12% per annum has been deduced for the female population, and 10% for the males.

The age dependent mortality rates for the female population have been tabulated using two different ages at sexual maturity and two durations of breeding cycle. Assuming the age at sexual maturity to be five years with the first offspring at six years the immature female mortality rate would be approximately 50%.

Assuming the above age at sexual maturity and that the Area I sample is representative of the catch then 25% of the catch is composed of immature specimens; a figure which accords well with the average annual catch of immature animals and the expected proportion prone to capture under the existing regulations. It is interesting to note that the female adult mortality rate of S. Georgia population between the years 1925–31 was assessed by Wheeler (1934) at 13% per annum and the theoretical immature mortality rate at approximately 50%; it will be seen that the adult female mortality rate for the present Area I sample was found to be in close agreement with these figures. With the age at sexual maturity at 5 years and the fertility rate 25% the above figures are exactly those required to keep the population stable in size. They also approximate to the figures for the apparent mortality rate which would be obtained by sampling an increasing population with a negligible mortality rate.

From the statistical analyses made by Hylen, Jonsgård, Pike & Ruud (1955) it may be noted that the peak catches are obtained according to the baleen plate data from age group 3 for females and age group 4 for males. According to the ear plug data from Area I the peak catches were obtained from the age groups 4–6 years in respect of females and 6–8 years in respect of males. This discrepancy may be partly explained by a difference between the mean total body lengths in the two populations, but is probably mainly due to the increased proportion of young animals in the population outside the " Sanctuary " the adult mortality rate of which was estimated to be 25%.

From the Hylen *et al.* analysis it appears that the population has become sexually mature at an earlier age in recent years. If Jonsgård's (1952) body length figure of 67 ft. at sexual maturity is applied to the growth curve of the Area II sample it will be seen to cut the x ordinate at the 8th lamination giving an age at sexual maturity of 4 years.

The oldest specimen recorded in the present sample was 42 years old and in this respect it is necessary to draw attention to a paper by Simons (1957) in which he states that in an unmolested Humpback Whale population the life span was very low. He bases his comments on the fact that only a small proportion of his sample of 146 individuals had attained an age greater than 14 years and that only 1 had reached the age of 29. It will be noted that his sample size for both sexes is smaller than the Area I sample. Under the conditions of Model 1 only 13% of the Area I population is over 14 years old and only 2·4% over 25 years old; the latter figure embraces all ages between 26 and 30, so the figure for the 29-year-olds is more likely to be ½%. These figures give no exact indication of the maximum life span of the animals. The question as to whether or not the material described in the present paper represents a random sample can be judged from Text-figs. 9 & 10. In Text-fig. 9 the age frequencies are plotted at intervals of two years, i.e. the approximate breeding cycle. It will be seen that males and females are present in each group in comparable numbers except that the peak value for males occurs two years later than that of the females. The left-hand side of the curve is much steeper than that of the right in both sexes notwithstanding that all the animals represented are above the permitted size limit. This effect is not due to any lack of randomness in the sample, nor to any length discrimination on the part of the gunners in the whaling fleet, both of which ideas have been suggested to explain the phenomenon in other samples. The steepness of the left-hand side of the curve is due to the fact that in the immature age groups the length variation is both relatively and absolutely greater than that of the adults, the standard deviation per age group in the sample being in the region of 5 ft.; thus a significant proportion of the immature animals is below the permitted size limit and therefore absent from the sample. As might be expected this effect is observable at a greater age in the males than in the females. In Text-fig. 10 the total frequencies of male and females have been plotted at two-yearly intervals. The dotted line represents the age frequency distribution of a hypothetical population of whales breeding every two years in which every individual becomes sexually mature at six years and in which the age frequency distribution remains stable with a constant mortality rate. Such a hypothetical population is perhaps unrealistic but the shape of the curve does indicate that the age frequency distribution of the sample approximates to that of a theoretically possible whale population. It is reasonable to assume that the sample is randomly drawn from a population with the above biological characteristics. If Simon's material is assumed to represent a truly random sample of the population then it would be statistically unlikely for more than one specimen in the sample of 146 females to be 29 years old, even if the maximum life span was 42 years or more.

Of the 12 Blue Whale ear plugs in the present collection only two were taken from animals more than 2 years old; 1 was from an animal 6 years old and the other 12 years old.

The above figures are based on the assumption that the ear plug laminae are formed at the rate of 2 per year but with the possible formation of one lamination per year the values would have to be doubled. For the purpose of estimating changes in the population structure the actual rate of laminar formation would appear to be immaterial provided the error, if any, is constant from year to year and age group to age group. From this point of view the ear plug is probably a more reliable guide to age than the ovary. The assumption on which the life tables were estimated i.e. that the size of the population is a constant number from year to year, is clearly to be regarded as no more than a crude first approximation to the actual form of population growth. However, with the present set of data it is necessary, for estimation purposes to make some such an assumption for it is not possible to deduce from data of one single year whether the population size is increasing, decreasing or static. It is evident that a more refined analysis of population growth can be applied only to extensive acts of data obtained in several successive years.

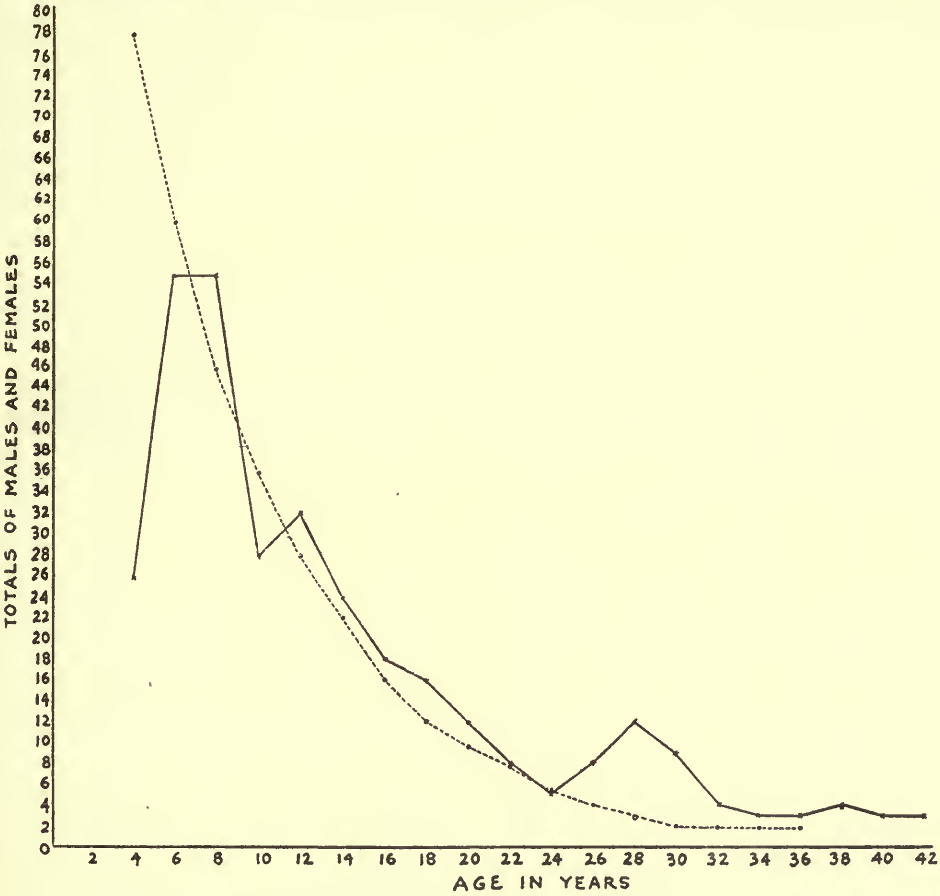


FIG. 10. Age distribution of a sample of fin whales *Balaenoptera physalus*. Sample distribution = X. Theoretical population distribution = o.

ACKNOWLEDGMENTS

Grateful acknowledgments are due to H.M. Ministry of Agriculture and Fisheries Whaling Inspectors aboard the factory ships *Balaena, Southern Harvester* and *Southern Venturer* during the Pelagic Whaling Season 1955–56 upon whose collections this report is based. Thanks are due to the National Institute of Oceanography for making available to us the material so collected. We wish particularly to express our appreciation to Mr. M. R. Clarke for the excellent set of data provided in his log, of which only the most obviously relevant details have been reproduced in our tables. We should also like to thank Messrs D. W. Cooper and M. G. Sawyers for the microscope and photomicrographic work involved and Miss J. R. Proctor for carrying out most of the computation. Finally we wish to thank Mr. J. G. Skellem and Dr. F. C. Fraser for their helpful criticism.

Masaharu Nishiwakis' " Age characteristics of Ear Plugs of Whales " reprinted from the *Scientific Reports of the Whales Research Institute*, No. 12, 1957 was received after completion of the foregoing account. It is gratifying to see that his results, based on a much smaller sample are in general agreement with the above. His new figure of 64 ft., for the age at sexual maturity of female Fin Whales does not coincide with previously published figures but if applied to Text-Fig. 3 of the present paper, it would give an age at sexual maturity of 4–5 years, which is identical with his own published result.

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APPENDIX

Table A.—*Female Antarctic Fin Whales* Balaenoptera physalus *Sample Area I*

Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)
1284	58	5	2½	58
863	63	6	3	32
1714	65	6	3	27
352	67	6	3	36
1820	68	6	3	25
2013	58	7	3½	58
1200	59	7	3½	59
1850	61	7	3½	30
739	63	7	3½	30
1785	64	7	3½	25
1819	68	7½	3¾	35
648	69	7	3½	37
601	69	7	3½	45
1707	58	8	4	58
652	58	8	4	58
776	60	8	4	25
1856	60	8	4	30
871	65	8	4	30
1454	66	8	4	26
2059	60	9	4½	—
1864	60	9	4½	33
1930	61	9	4½	31
2126	62	9	4½	27
1748	63	9	4½	24
1108	64	9	4½	48
933	65	9	4½	33
1118	65	9	4½	—
1248	67	9	4½	37
1036	68	9	4½	40
1813	68	9	4½	33
519	60	10	5	34
2043	60	10	5	23
1749	63	10	5	37
1898	63	10	5	35
1247	66	10	5	30
859	67	10	5	35
1279	69	10	5	34
1196	73	10	5	33
1937	62	11	5½	14
515	64	11	5½	—
1890	65	11	5½	40
1821	65	11	5½	62
1817	66	10	5	33
935	66	11	5½	30
1165	68	11	5½	46
1167	61	12	6	18
1208	63	12	6	34
448	67	12	6	44
1320	67	12	6	44
1034	67	12	6	35
1209	68	12	6	49
786	73	12	6	45
2095	76	12	6	40
1812	64	13	6½	—
2097	65	13	6½	—
670	72	13	6½	50
656	67	14	7	36
2128	67	14	7	40
1968	68	14	7	40
1784	68	14	7	35

TABLE A—*cont.*

Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)	Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)
906	70	14	7	34	529	70	26	13	53
1901	70	14	7	34	1625	70	27	13½	42
1079	72	14	7	—	1816	73	27	13½	73
1811	67	15	7½	40	1704	73	27	13½	91
660	71	15	7½	52	1040	68	28	14	78
855	72	15	7½	43	743	74	28	14	78
1285	70	16	8	53	1169	68	29	14½	94
1775	71	16	8	34	747	69	29	14½	42
2044	72	16	8	50	1966	73	30	15	70
703	72	16	8	60	1280	70	31	15½	75
1675	72	16	8	40	672	70	32	16	80
1927	72	16	8	40	1710	71	32	16	66
562	73	16	8	56	1630	74	32	16	87
1823	77	16	8	42	486	75	32	16	52
513	69	17	18½	37	2134	76	32	16	55
737	71	17	8½	60	1628	75	33	16½	60
1854	74	17	8½	32	1633	67	34	17	74
784	68	18	9	25	482	75	34	17	70
896	71	18	9	34	780	75	35	17½	63
2136	71	18	9	42	741	67	36	18	70
1085	73	18	9	49	712	72	36	18	67
1964	74	19	9½	47	1933	72	36	18	45
898	70	20	10	50	2007	72	36	18	65
597	70	20	10	40	593	73	36	18	63
2099	70	20	10	50	1669	75	36	18	33
674	72	20	10	51	1931	76	37	18½	50
1664	72	20	10	60	1670	73	39	19½	73
646	74	21	10½	63	1044	68	40	20	60
1083	70	22	11	34	2015	70	40	20	75
1779	71	22	11	38	937	72	40	20	60
2122	72	22	11	29	1706	72	40	20	94
714	71	22	11	70	488	73	40	20	90
1739	73	23	11½	72	2085	72	42	21	70
894	71	24	12	56	1042	74	42	21	92
1788	71	24	12	—	2130	69	43	21½	53
1892	72	24	12	—	438	72	45	22½	58
700	72	24	12	27	906	75	46	23	145
603	73	24	12	53	1634	72	50	25	73
1366	73	24	12	—	1425	81	50	25	39
434	78	34	12	80	1250	69	54	27	75
398	67	24	12	67	1357	77	54	27	96
595	71	25	12½	—	1703	69	55	27½	69
749	71	25	12½	59	1163	70	56	28	60
745	70	26	13	—	1938	72	56	28	71
2099	70	26	13	50	1352	72	56	28	56
867	72	26	13	17	2009	75	66	33	93
1358	74	26	13	74	706	75	70	35	88
478	77	26	13	85	358	73	80	40	120

TABLE B.—*Male Antarctic Fin Whales* Balaenoptera physalus *Sample Area I*

Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)
1278	55	3½	1¾	—
9423	58	4	2	20
2047	60	4	2	26
1700	64	6	3	14
2041	58	7	3½	27
560	58	7	3½	58
925	68	8	4	24
1972	61	8	4	30
1818	61	9	4½	41
1932	61	9	4½	31
1110	62	9	4½	41
400	63	9	4½	24
440	64	9	4½	38
1786	64	9	4½	34
1115	67	9	4½	25
1781	65	9	4½	31
1702	61	10	5	56
1857	63	10	5	25
900	66	10	5	68
947	66	10	5	32
1858	67	10	5	43
517	62	11	5½	43
1772	63	11	5½	29
1201	69	11	5½	—
1638	63	12	6	41
564	64	12	6	38
1598	65	12	6	30
941	66	12	6	45
1000	68	12	6	30
974	62	13	6½	60
1296	64	13	6½	47
1244	64	13	6½	40
931	65	13	6½	37
2057	65	13	6½	42
1862	65	13	6½	37
2045	67	13	6½	43
1194	69	13	6½	38
708	62	14	7	43
1206	62	14	7	48
558	65	14	7	48
865	65	14	7	35
1243	66	14	7	27
1742	66	14	7	55
1203	67	14	7	30
2005	67	14	7	13
1663	68	14	7	42
1205	64	15	7½	38
1827	66	15	7½	42
1894	66	15	7½	27
356	66	15	7½	43
904	67	15	7½	50
650	63	16	8	36
1824	65	16	8	60
394	65	16	8	70
525	66	16	8	48
1886	67	16	8	53
1202	67	16	8	63
1116	67	16	8	35
1783	68	16	8	45
2053	68	16	8	55
1629	65	17	8½	60
1667	66	17	8½	55
1453	67	17	8½	35
1327	67	17	8½	45
476	69	17	8½	50
531	67	17	8½	50
1637	69	17	8½	50
869	69	18	9	69
654	66	19	9½	38
658	71	19	9½	57
521	65	20	10	26
1038	66	20	10	62
1032	66	20	10	53
902	53	20	10	53
1081	67	20	10	40
523	68	21	10½	—
1363	73	21	10½	40
490	66	22	11	46
1355	66	22	11	62
857	68	22	11	60
939	71	22	11	54
1257	71	22	11	—
1671	67	40	20	50
1861	70	40	20	100
1356	66	42	21	77
927	66	43	21½	78
976	68	43	21½	77
1326	65	43	21½	42
1198	66	44	22	80
1121	66	44	22	50
716	68	45	22½	38
1238	66	46	23	85
1860	68	46	23	94
1825	67	49	24½	65

TABLE B—*cont.*

Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)	Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)
1112	64	50	25	65	1902	68	23	11½	—
1452	68	50	25	50	2049	71	23	11½	57
1745	71	50	25	85	1635	64	24	12	35
1776	65	52	26	52	480	67	24	12	58
1978	67	52	26	68	1071	68	24	12	55
710	65	53	26½	65	1451	70	24	12	40
568	62	54	27	88	1274	74	24	12	45
1077	66	54	27	46	363	63	25	12½	45
1113	68	54	27	58	1286	67	25	12½	43
605	66	55	27½	83	1251	70	25	12½	56
442	71	59	28½	63	1674	67	26	13	43
1636	63	56	28	62	1743	65	26	13	—
1627	65	59	28½	90	1822	79	26	13	45
406	65	56	28	62	945	64	27	13½	57
1741	65	58	29	67	2051	66	27	13½	53
1744	68	58	29	40	1599	63	28	14	63
396	67	59	29½	77	1111	67	28	14	62
662	66	60	30	85	1965	69	28	14	62
1073	72	60	30	120	1239	68	29	14½	82
1855	68	61	30½	65	704	70	29	14½	—
1705	73	62	31	80	772	65	30	15	65
1353	70	63	31½	50	1740	66	30	15	48
527	65	66	33	80	1888	66	30	15	83
702	70	67	33½	68	1815	69	30	15	47
1252	73	70	35	—	2083	65	31	15½	70
1120	65	71	35½	100	1207	68	31	15½	68
416	68	75	37½	—	2120	65	32	16	60
570	67	76	38	130	1423	70	33	16½	40
788	66	76	38	84	1666	66	35	17½	33
1075	64	85	42½	72	1893	64	36	18	58
676	64	83	41½	95	1450	69	36	18	80
1325	64	23	11½	42	1240	70	36	18	80
1777	65	23	11½	46	1597	71	36	18	40
2132	65	23	11½	40	361	65	37	18½	48
1774	67	23	11½	65	1626	67	38	19	60
2087	68	23	11½	33	1671	67	40	20	50

TABLE C.—*Female Antarctic Fin Whales* Balaenoptera physalus *Sample Area II*

Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)	Factory ship
1480	60	3	1½	20	*Southern Venturer*
A1493	62	5	2½	25	,, ,,
A1231	67	5	2½	30	*Balaena*
—	63	6	3	—	,,
—	61	7	3½	18	,,
1259	59	7	3½	28	,,
A1485	62	7	3½	30	*Southern Venturer*
1236	74	8	4	32	*Balaena*
—	65	9	4½	34	,,
1745A	65	9	4½	25	*Southern Venturer*
1239	66	9	4½	40	*Balaena*
A1261	67	10	5	40	,,
A1234	67	10	5	40	,,
—	68	16	8	35	,,
—	70	11	5½	—	,,
A1232	70	11	5½	40	,,
A1250	70	12	6	37	,,
A1550	70	12	6	—	*Southern Venturer*
1741	68	12	6	45	,, ,,
A1532	74	12	6	—	*Balaena*
A1255	71	12	6	—	,,
A1539	72	13	6½	40	,,
A1228	72	14	7	50	,,
A1233	72	15	7½	43	,,
—	68	16	8	95	,,
1251	76	18	9	50	,,
1253	76	19	9½	34	,,
A1486	72	20	10	58	*Southern Venturer*
—	74	21	10½	55	*Balaena*
1252	75	21	10½	80	,,
A1494	72	21	10½	58	*Southern Venturer*
A1240	72	22	11	78	*Balaena*
1247	78	22	11	90	,,
A1490	75	24	12	—	*Southern Venturer*
1230	73	28	14	—	*Balaena*
A1348	77	29	14½	78	,,
A1547	75	30	15	65	,,
1478	73	31	15½	88	*Southern Venturer*
—	75	32	16	67	*Balaena*
A1235	75	32	16	85	,,
1747	73	32	16	55	*Southern Venturer*
A1242	73	33	16½	48	*Balaena*
—	75	34	17	100	,,
1742	68	38	19	85	*Southern Venturer*
—	72	42	21	105	*Balaena*
A1739	75	43	21½	64	*Southern Venturer*
A1536	78	44	22	60	,, ,,
A1538	77	46	23	60	*Balaena*
1243	74	47	23½	115	,,
A1748	76	48	24	64	*Southern Venturer*
A1740	74	50	25	87	,, ,,
A1547	75	30	15	65	*Balaena*
A1555	79	53	26½	75	,,
A1534	75	62	31	100	,,
—	78	66	33	83	,,

TABLE D.—*Male Antarctic Fin Whales* Balaenoptera physalus *Sample Area II*

Whale number	Total length (ft.)	Number of laminae	Estimated age (years)	Length of core (mm.)	Factory ship
A1487	55	5	2½	20	*Southern Venturer*
—	63	8	4	10	*Balaena*
1488	63	8	4	36	*Southern Venturer*
—	63	9	4½	35	*Balaena*
1497	63	9	4½	53	*Southern Venturer*
1416	65	9	4½	58	,, ,,
A1749	55	9	4½	30	,, ,,
A1492	63	10	5	53	,, ,,
1475	66	11	5½	30	,, ,,
—	65	14	7	—	*Balaena*
—	70	16	8	50	,,
1744	69	16	8	24	*Southern Venturer*
—	68	19	8½	84	*Balaena*
1484	71	19	9½	80	*Southern Venturer*
—	71	20	10	24	*Balaena*
—	71	20	10	62	,,
—	70	22	11	50	,,
—	69	23	11½	35	,,
1735	69	23	11½	53	*Southern Venturer*
1737	70	31	15½	35	,, ,,
1495	69	30	15	63	,, ,,
1489	72	32	16	50	,, ,,
—	68	34	17	47	*Balaena*
—	70	34	17	—	,,
—	70	36	18	30	,,
—	69	40	20	75	,,
—	70	40	20	43	,,
—	70	43	21½	40	,,
—	71	44	22	24	,,
1736	67	45	22½	95	*Southern Venturer*
A1488	67	50	25	36	,, ,,
1481	65	59	28½	55	,, ,,
A1738	76	63	31½	80	,, ,,

TABLE E.—*Unlogged Antarctic Fin Whales* Balaenoptera physalus

Males		Females	
Whale number	Estimated age (years)	Whale number	Estimated age (years)
1600	16	1168	4
1321	12	773	4½
1??5	9½	474	4
890	32½	757	10½
1715	23½	912	4½
1969	9	1164	13
—	10	1319	1½
—	17½	480	4
—	11½	—	9
—	8½	—	18½
—	19	—	9
—	12	—	11
—	12½	—	9½
—	12½	—	16
—	12½	—	6
—	4½	—	6½
—	4	—	8
—	—	—	6½
—	—	—	15
—	—	—	7½

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PLATE 5

A series of ear plugs from female Fin Whales showing progressive lengthening of the core.

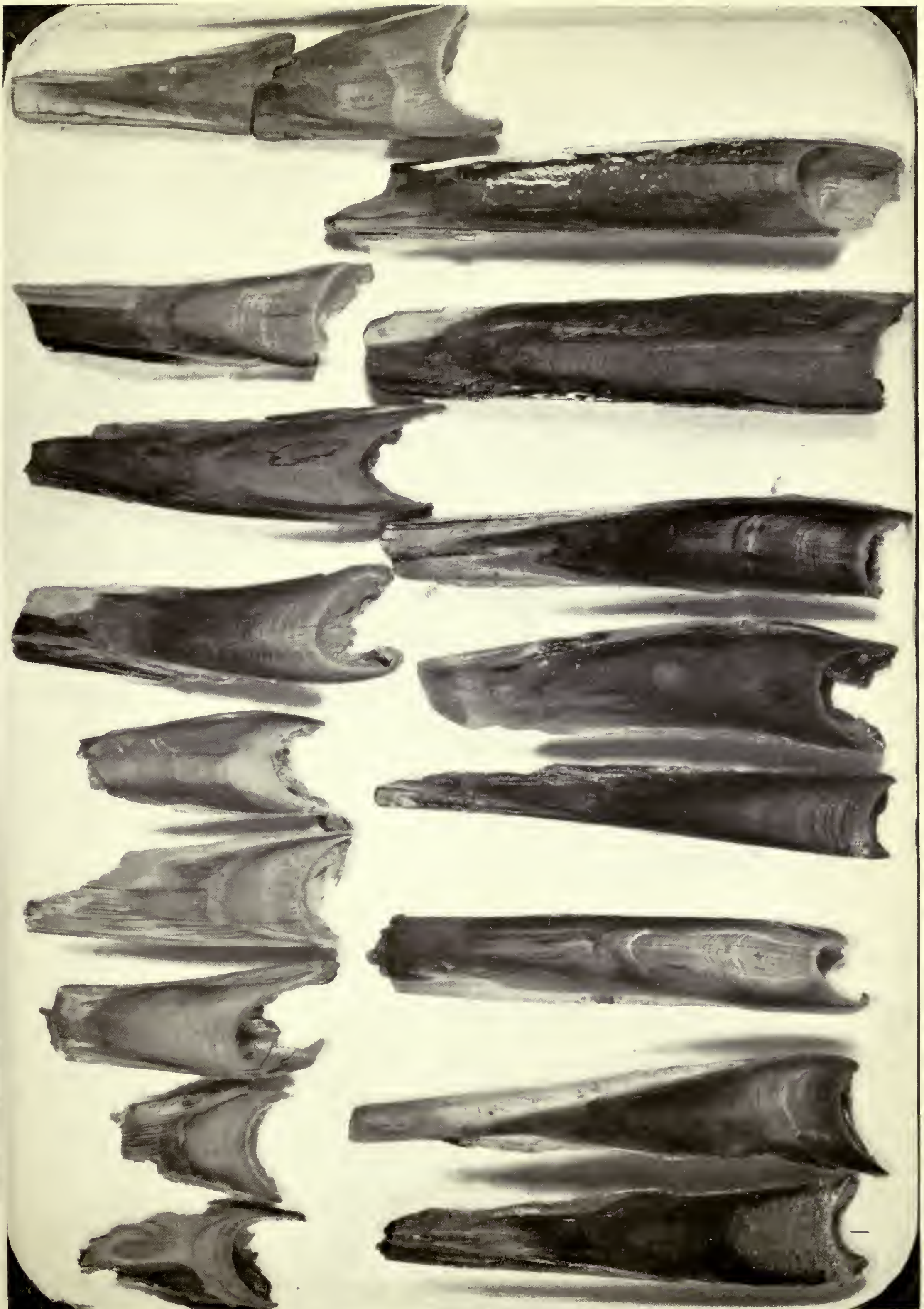
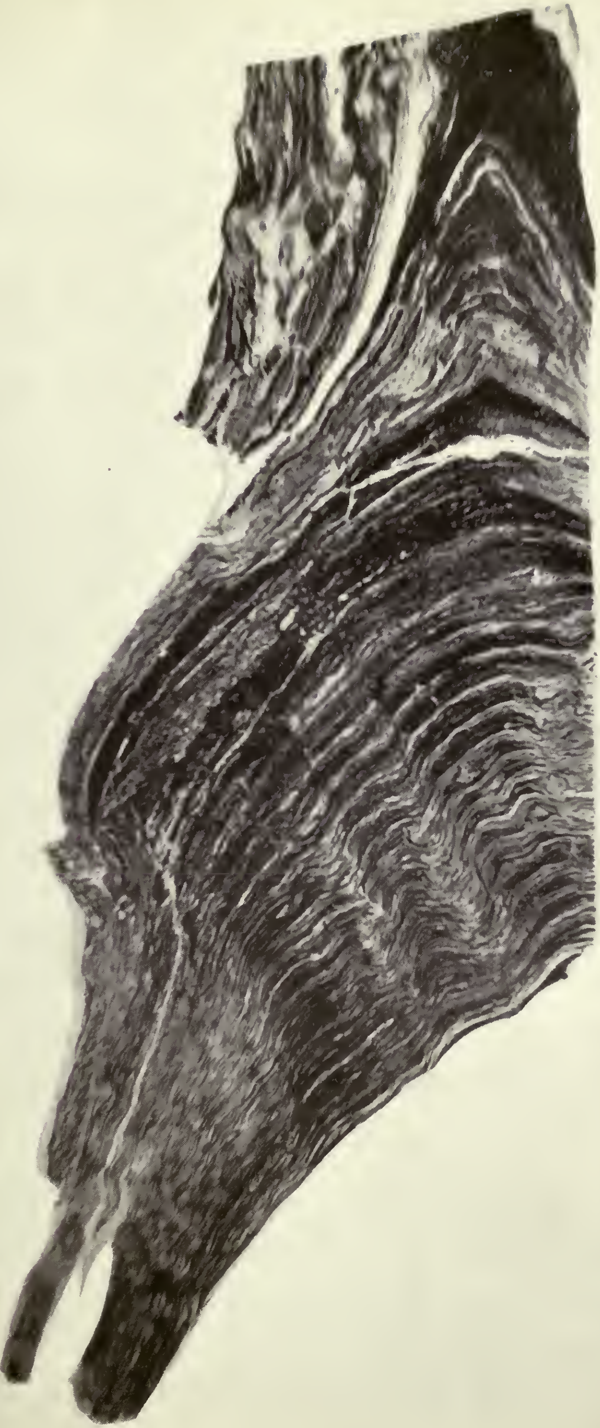


PLATE 6

A longitudinal section through the base of an abnormal ear plug showing coarse and fine laminations. Mag. × 20.



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THE MONOTYPIC GENERA OF CICHLID FISHES IN LAKE VICTORIA

PART II

AND

A REVISION OF THE LAKE VICTORIA *HAPLOCHROMIS* SPECIES (PISCES CICHLIDAE)

PART III

P. H. GREENWOOD

BULLETIN OF
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P. H. GREENWOOD

Department of Zoology, British Museum (Natural History)

Pp. 163–218 ; 16 *Text-figs.*

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THE MONOTYPIC GENERA OF CICHLID FISHES IN LAKE VICTORIA, PART II[1]

By P. H. GREENWOOD[2]
British Museum (Natural History), London

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A REVISION of the four endemic monotypic cichlid genera of Lake Victoria, *Macropleurodus bicolor* (Blgr.), *Platytaeniodus degeni* Blgr., *Hoplotilapia retrodens* Hilg., and *Paralabidochromis victoriae* Greenwood has already been published (Greenwood, 1956). These species differ from *Haplochromis* in various dental characters. Unlike the other monotypic genera, *Astatoreochromis alluaudi* is not confined to the Lake Victoria basin; its range includes Lakes Edward, George, Nakavali and Kachira (Trewavas, 1933). Furthermore, *Astatoreochromis* differs from *Haplochromis* only in having an increased number of spines in the anal fin; the oral dentition is typically that of a non-piscivorous *Haplochromis*.

Genus *ASTATOREOCHROMIS* Pellegrin, 1903

Astatoreochromis Pellegrin, 1903, *Mém. Soc. zool. France*, **16**, 385; *Idem*, 1905, *ibid.* **17**, 185, pl. XVI, fig. 2; *Idem*, 1910, *ibid.* **22**, 297; Regan, 1922, *Proc. zool. Soc., London*, 188; Fowler, 1936, *Proc. Acad. nat. Sci. Philad.* **88**, 333, fig. 138 (mis-spelt *Astatore*); Poll, 1939, *Explor. Parc. Nat. Albert, mission* H. Damas (1935–36), fasc. 6, 1–73. *Haplochromis* (part) Boulenger, 1907, *Fish, Nile*, 505 pl. XC, fig. 4; *Idem*, 1911, *Ann. Mus. Genova* (3), **5**, 71; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 305, fig. 206.

Type species. Astatoreochromis alluaudi Pellegrin, 1903.

Diagnosis. Astatoreochromis differs from *Haplochromis* only in having four or more spines in the anal fin. From other genera in the *Haplochromis* group with more than four anal fin spines, *Astatoreochromis* is distinguished by the absence of a marked antero-posterior differentiation in the form of the premaxillary teeth.

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[2] Formerly East African Fisheries Research Organization, Jinja, Uganda.

In comparison with the *Haplochromis* of Lakes Victoria, Edward, and Kachira, *Astatoreochromis* shows an increased ratio of spinous to branched rays in the dorsal and anal fins. From other *Haplochromis*-like genera in these lakes, *Astatoreochromis* differs both in having more anal fin spines and in the nature of its oral dentition.

Discussion. As Boulenger (1907) pointed out, the principal diagnostic character for *Astatoreochromis* cannot be considered trenchant because some four-spined specimens of normally three-spined *Haplochromis* species have been recorded. He cites as an example an aberrant *H. desfontainesi* from Tunisia. Nevertheless, throughout the very numerous species of *Haplochromis* it is very exceptional to find an individual with more (or less) than three anal fin spines and as yet no specimens of *Astatoreochromis* with less than four anal spines have been found. It cannot be denied that *Astatoreochromis* and *Haplochromis* are closely related (as are *Haplochromis* and the other monotypic genera of Lakes Edward and Victoria) and it might seem that little is to be gained from recognizing *Astatoreochromis* as a distinct genus.

However, *Astatoreochromis* differs from the *Haplochromis* of Lakes Victoria and Edward in four other characters which, if taken together, may indicate that it has a different lineage from these species. In an earlier paper (Greenwood, 1954) I drew attention to the form of the pharyngeal apophysis in *Astatoreochromis* and showed that it resembles the apophysis occurring in *Haplochromis vanderhorsti* Greenwood (Malagarasi River) and *H. mahagiensis* David & Poll (Lake Albert). The other Victoria species with enlarged pharyngeal bones (*H. ishmaeli* Blgr. and *H. pharyngomylus* Trewavas) have a different apophyseal form. A summary of these observations is given in Text-fig. 2.

Contrary to my earlier views, I now consider that, taken by itself, apophyseal form is of doubtful value as an indicator of phyletic relationship. For example, both the *H. mahagiensis-H. vanderhorsti* and the *H. ishmaeli-H. pharyngomylus* types of apophysis are found in Lake Nyasa *Haplochromis* with enlarged pharyngeal bones; *Haplochromis placodon* Regan (a species with hypertrophied pharyngeals) has the "*ishmaeli*" type whilst *H. sphaerodon* Regan, *H. latristriga* (Günther) and *H. selenurus* (Regan) (species with less massive pharyngeals) have the "*mahagiensis*" type. There is no evidence to suggest that Nyasa fishes with "*mahagiensis*"-like apophyses are more closely related to one another than to *H. placodon*, or that they represent an exotic element within the Nyasa flock. Certainly there is no indication of their being related to the *H. mahagiensis-H. vanderhorsti* species group. Thus, one must conclude that similarity of apophyseal form is yet another example of convergent evolution, at least at an inter-group level.

Considering *Astatoreochromis* in relation to the cichlid species flocks of Lakes Victoria and Edward it is clear that this genus does not conform to the general morphological pattern of the endemic species and genera. Three characters, the shape of the caudal fin, the coloration and the high number of anal ocelli, set *Astatoreochromis* apart. Excepting *H. melanopterus* (a species of doubtful validity, see Greenwood, p. 192) all the endemic *Haplochromis* of Lake Victoria have a truncate or subtruncate caudal fin; the caudal of *Astatoreochromis* is distinctly rounded.

A considerable variety of colour and colour patterns is exhibited by the endemic

Haplochromis, but all can be broken down into various combinations of several basic types. The golden-green ground colour of *Astatoreochromis* does not occur in any endemic species. The third outstanding characteristic of *Astatoreochromis* is the high number of ocelli on the anal fin of male fishes. Not only are the ocelli more numerous than in *Haplochromis*, but they are arranged in three or four horizontal rows ; it is extremely rare to find more than two rows in any *Haplochromis* from Lake Victoria or Edward.

In all these characters, *Astatoreochromis* resembles *H. vanderhorsti*. There is also one other point of close inter-specific resemblance ; both species show only slight dimorphism in the coloration of the two sexes. In contrast the coloration of Lake Victoria *Haplochromis* is markedly dimorphic.

Thus, although the form of the pharyngeal apophysis alone is of doubtful value in showing phyletic relationships, I consider that the additional evidence supports my original conclusion that *Astatoreochromis* was derived from an *H. vanderhorsti*-like stem. The two other Victoria species with enlarged pharyngeal bones and dentition (*H. ishmaeli* and *H. pharyngomylus*) are apparently related to one another. Their origin was probably by way of two forms represented in the present lake by a generalized species formerly confused with *H. michaeli* [see Greenwood, 1954 and 1956*a*], but now known to be an undescribed species and a species partly advanced towards extreme hypertrophy of the pharyngeal mill (*H. obtusidens*).

The apparently distinct origin of *Astatoreochromis alluaudi* in relation to the rest of the Victoria-Edward *Haplochromis* species flock is a further and perhaps more fundamental reason for maintaining the species as a distinct genus.

Astatoreochromis alluaudi Pellegrin, 1903

(Text-fig. 1)

For synonymy see under genus.

Lectotype. A female 122 mm. S.L. from the Kavirondo Gulf, Lake Victoria ; Reg. No. 04, 137 of the Paris Museum.

Description. From the available material it seems that only two characters (length of the caudal fin and the extent to which the lower pharyngeal bones are hypertrophied) show clear-cut differences between populations inhabiting the various lakes. These two characters will be treated separately but all others are given for the species as a whole.

The general species description is based on the following material : Lakes Victoria and Kyoga (including the Victoria Nile), 77 specimens, 20–163 mm. S.L. (of which 40, including the four syntypes, were used in obtaining proportional measurements) : Lakes Edward and George 11 specimens 24·0–80·0 mm. S.L.; Lake Nakavali, 18 specimens, 50–137 mm. S.L. (of which 11 were used for proportional measurements) ; Lake Kachira, three specimens 66–78 mm. S.L.

Depth of body 33·8–43·3 per cent of standard length, length of head 32·1–40·0, mean (M) = 35 per cent. Dorsal head profile fairly steeply sloping, straight or somewhat decurved, becoming concave in larger individuals.

Preorbital depth, showing slight positive allometry with standard length, 11·1–17·5 (M = 15·0) per cent of head length, least interorbital width 25·2–31·7 (M = 28·3) per cent. Snout as broad as long, its length 25·0–33·3 (M = 29·2) per cent of head. Eye diameter shows negative allometry with standard length, being 31·5–23·2 (M = 27·2) per cent of head in fishes 20–80 mm. S.L. and 24·3–18·8 (M = 22·1) per cent in larger individuals. Depth of cheek positively allometric with standard length; 12·8–26·0 (M = 21·3) and 20·0–27·9 (M = 24·2) per cent of head in the two size groups mentioned above.

Caudal peduncle 11·0–15·2 per cent of standard length, its length/depth ratio 1·0–1·4 (modal range 1·0–1·1) or, rarely, deeper than long.

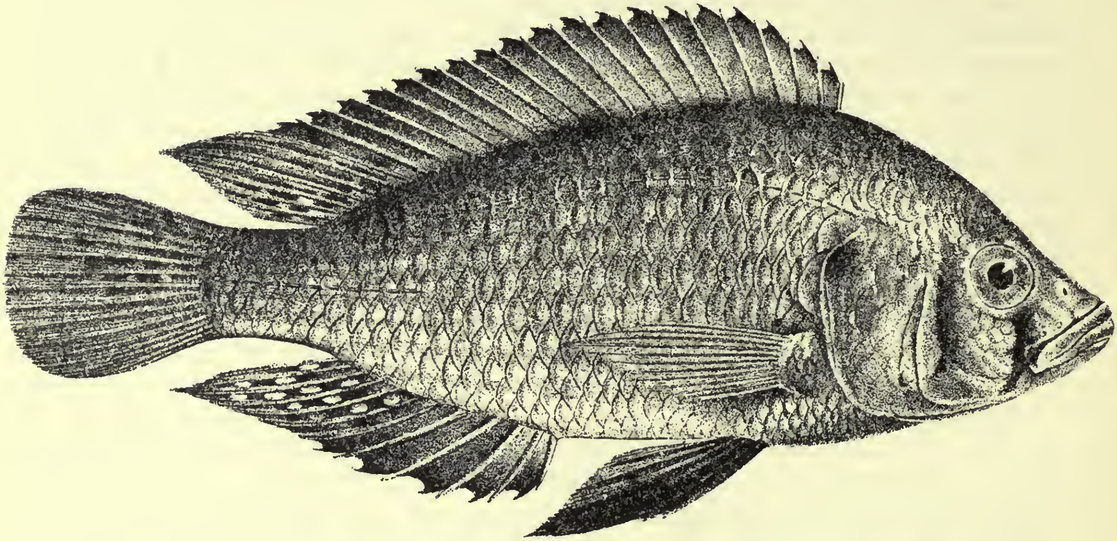

FIG. 1. *Astatoreochromis alluaudi alluaudi* (from Boulenger, *Fishes of the Nile*).

Mouth horizontal or slightly oblique. Jaws equal anteriorly or, occasionally, lower somewhat projecting; posterior tip of the maxilla reaching or almost reaching the vertical to the anterior orbital margin. Lower jaw 35·0–45·3 (M = 40·0) per cent of head length and 1·3–2·0 (rarely) times as long as broad (modal range 1·5–1·6).

Gill rakers short and stout; 8 or 9 (occasionally 10, rarely 7) on the lower limb of the first gill-arch.

Scales ctenoid; lateral line with 30 (f.12), 31 (f.21), 32 (f.20) or 33 (f.2) scales; cheek with 3 or 4 (occasionally 5) series; 4 or 5 (occasionally 6) scales between the origin of the dorsal fin and the lateral line; 4–6 (rarely 7) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.2), 24 (f.4), 25 (f.15), 26 (f.68), 27 (f.11) or 28 (f.1) rays, comprising 16 (f.5), 17 (f.16), 18 (f.59), 19 (f.20) or 20 (f.1) spinous and 7 or 8 (rarely 9) branched rays. Anal fin with 11 (f.3), 12 (f.67), 13 (f.30) or 14 (f.2) rays comprising

4 (f.28), 5 (f.63) or 6 (f.11) spinous and 7 or 8 (rarely 6 or 9) branched rays. Pectoral fin shorter than the head, 22·3–29·4 per cent of standard length.

Caudal fin rounded, longer in fishes from Lakes Nakavali, Edward and George than in those from Lake Victoria; namely: length of caudal fin in Victoria specimens (N = 41) 21·4–28·5 (Mean 24·3) per cent of standard length; in Lake Nakavali fishes (N = 4) 24·0–31·6 (M = 27·4) per cent, and in Lake Edward fishes (N = 9), 24·0–31·6 (M = 27·0). This fin was damaged in two of the three specimens from Lake Kachira.

Pelvic fin with the first ray produced and extending to beyond the vent or as far as the spinous part of the anal fin.

Teeth. Even in the smallest specimen examined, the most posterior teeth in the upper jaw were unicuspid. In fishes less than 100 mm. S.L., the anterior and lateral teeth of the upper jaw and the entire outer series of teeth in the lower jaw are unequally bicuspid and relatively stout. In larger specimens, the dentition is a mixture of weakly bicuspid and unicuspid teeth; fishes over 140 mm. S.L. (and some smaller individuals) have only stout, unicuspid teeth in the outer series of both jaws. There are 28–56 (modal range 40–46) outer teeth in the upper jaw.

The small, tricuspid or unicuspid inner teeth are arranged in one or two rows.

Osteology. Vertebrae: 15 + 14 in the single specimen examined B.M. (N.H.) Reg. No. 1911.3.3.111, from Kakindu, Victoria Nile.

Neurocranial apophysis for the upper pharyngeal bones. The form of this apophysis was mentioned in the discussion on generic characters. Since the apophysis is of importance in defining cichlid genera, its variation and the probable factors influencing its variability in *Astatoreochromis* will be outlined briefly.

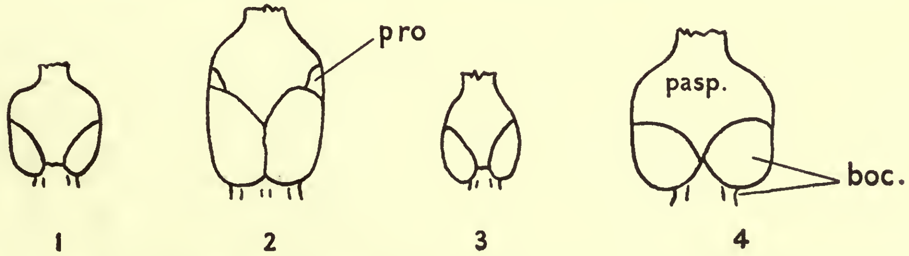

Fig. 2. Semi-diagrammatic representation of the shape and proportions of elements contributing to the upper pharyngeal apophysis in: (1) young *Astatoreochromis a. alluaudi*; (2) adult *A. a. alluaudi*; (3) adult *Haplochromis vanderhorsti*; (4) adult *Haplochromis ishmaeli*. Scale constant.

Although the shape and proportions of elements contributing to the apophysis are affected by the relative size of the pharyngeal bones, the characteristic group facies (see p. 170) is developed even in the absence of markedly hypertrophied pharyngeals (Text-fig. 2, (i)). In *A. alluaudi* it appears that the extent to which the basioccipital facets are enlarged and expanded depends primarily on the relative hypertrophy of the pharyngeals, and secondarily on the size of the fish. Thus, in two specimens from Lake Victoria, one, 73 mm. S.L. with weakly developed pharyngeals, has proportionately smaller basioccipital facets than the other, 63 mm. S.L. and with enlarged pharyngeal bones and teeth (cf. Text-fig. 2 (i) and 2 (ii)). Likewise, fishes 70 mm., 76 mm., and 80 mm. S.L., from Lake Edward, and two specimens 71 mm. and 82 mm. S.L. from Lake Nakavali all have weakly developed pharyngeals, and apophyses comparable with the 73 mm. fish mentioned above. In this size-range it would appear that the size of the pharyngeal bones is exerting full influence on apophyseal form.

The effect of overall size is demonstrated in a fish 125 mm. S.L. from Lake Nakavali. In this specimen the pharyngeal bones are weak in comparison with those of a comparable sized fish from Lake Victoria (cf. Text-fig. 3, lower row, left and right). Yet, the apophyseal form is similar in the two specimens except for a slightly smaller surface area in the Nakavali fish.

Lower pharyngeal bone triangular. The form of this bone (which depends on the degree to which it is hypertrophied) and the nature of its teeth show a marked difference between fishes from Lake Victoria (including Kyoga) and those from the other lakes (see Text-fig. 3). When specimens of equal sizes from different lakes are compared it is immediately obvious that those from Lake Victoria have more massive bones with a greater proportion of molariform teeth. As far as can be determined from available material there is a little geographical variation of this character in fishes from Lakes Edward, George, Nakavali and Kachira. In all these populations the bone is clearly less massive than in Lake Victoria fishes and there are fewer molariform teeth. When present, such teeth are generally confined to the two median rows ; any enlarged teeth in the lateral series are usually cuspidate.

The difference in pharyngeal bone size can be expressed quantitatively by using the ratio of head length to pharyngeal bone width (measured from tip to tip of the upper arms) ; it is, however, less impressive an indication of disparity in massiveness than an actual comparison of individual bones. The ratio for specimens from the various lakes is : *Victoria* (including Kyoga) ; 2·4–3·1 (Mean 2·7 ; 32 specimens examined) ; *Nakavali* : 2·6–3·6 (Mean 3·1 ; 16 specimens) ; *Edward and George* : 2·8–3·6 (Mean 3·0 ; 10 specimens) ; Kachira : 2·7–3·1 (Mean 3·0 ; three specimens).

As specimens of *A. alluaudi* from Lake Victoria cover a sufficiently wide size-range it is possible to determine ontogenetic changes in tooth form and in the proportions of the bone. In the smallest specimen (20 mm. S.L.) the two median tooth-rows are composed of enlarged but cuspidate teeth and the bone is relatively coarse (Text-fig. 3 top row, left). With increasing size, the bone becomes proportionately stouter and the median teeth larger and blunter (Text-fig. 3 middle row, left), as do some of the teeth in the lateral rows. In the great majority of fishes over 60 mm. S.L., only the most lateral series of teeth, and those in the upper corners of the bone, remain slender and cuspidate. The number of such non-molariform teeth is even further reduced in fishes greater than 120 mm. S.L. Only seven of the 78 fishes examined had pharyngeal bones and dentition less hypertrophied than the modal condition for their respective size-groups.

Ontogenetic changes are less marked in *A. alluaudi* from the western lakes. The impression gained from these specimens is that the pharyngeal bones, apart

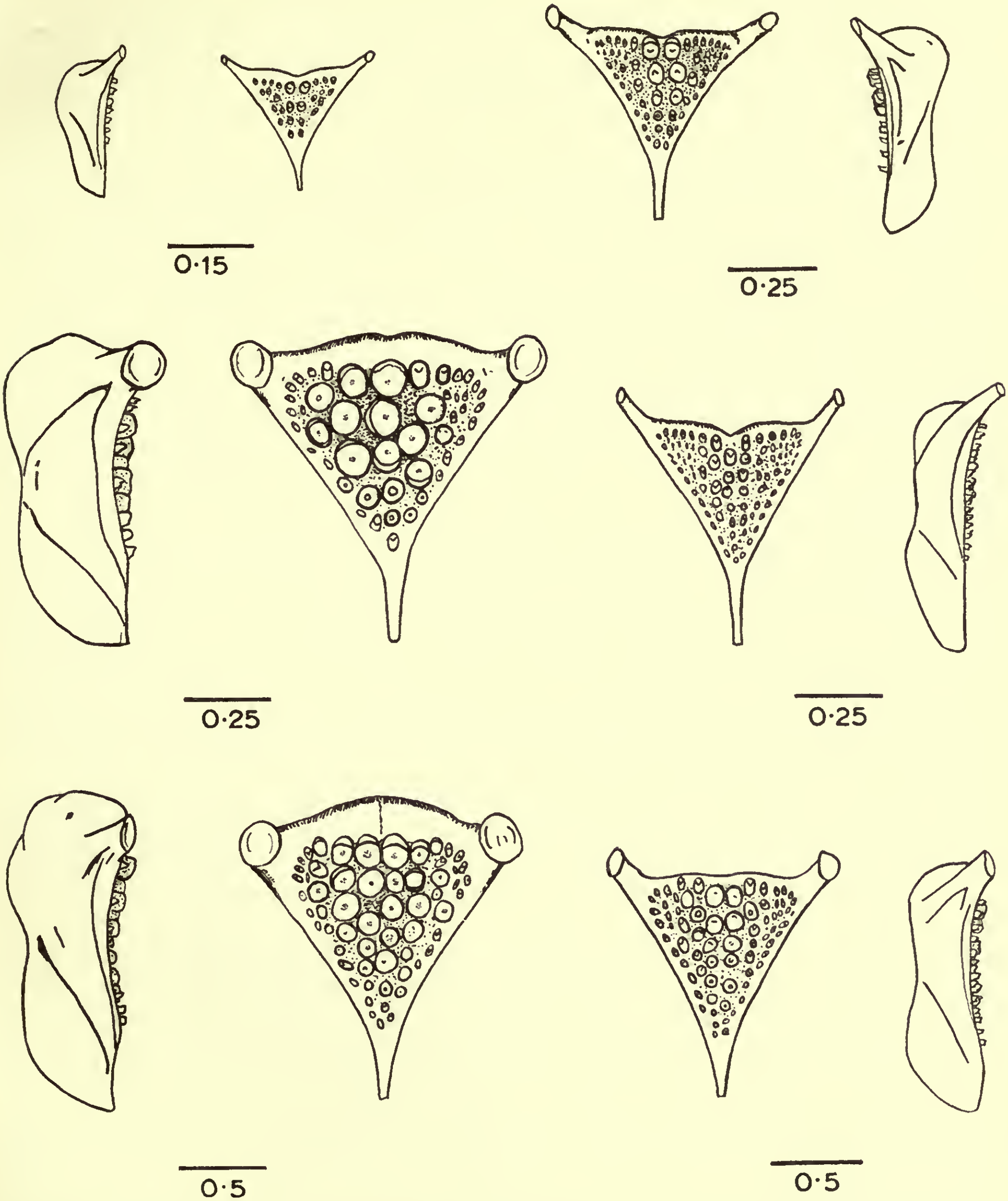

Fig. 3. Lower pharyngeal bones and teeth (lateral and occlusal views) of: Top row, left *Astatoreochromis a. alluaudi* 20 mm. S.L.; right, *A. a. alluaudi* 48 mm. S.L. Middle row, left, *A. a. alluaudi* 60 mm. S.L.; right, *A. a. occidentalis* (Lake Nakavali) 63 mm. S.L. Bottom row, left, *A. a. alluaudi* 120 mm. right, *A. a. occidentalis* (Lake Nakavali) 123 mm. S.L. Scale in centimetres.

from their greater size, may be compared with those of 20–30 mm. *A. alluaudi* from Lake Victoria.

Nothing is known about the epigenetics of *A. alluaudi* and little is known of the feeding habits of populations in lakes other than Victoria. It is therefore impossible to define the causal factors for the marked intra-specific, geographical difference in pharyngeal bones and teeth.

In Lake Victoria, *A. alluaudi* feed almost exclusively on Mollusca (see below) and particularly on the thick-shelled *Melanoides tuberculata.* Considering the extreme plasticity of bone and its response to intermittent pressure (see Murray, 1932; Weinmann & Sichner, 1947) it seems probable that the effects of crushing such prey might produce an adaptational thickening and strengthening of the pharyngeals. In this way, any genetical tendency towards pharyngeal hypertrophy (as manifest in the relatively coarse lower pharyngeals of post-larval *A. alluaudi*) would be reinforced. If, on the other hand, in the western lakes the species is not predominantly a mollusc eater, the adaptational stimulus for increased bone size would be less, and the bones might be relatively weak. Finally, the possibility of inter-populational genetic differences cannot be discounted, especially since the various lakes are geographically isolated.

Some data seem to add weight to the first, i.e. adaptational, hypothesis. The stomach and intestinal contents of 13 Lake Nakavali fishes have been examined; of these, two were empty. Five of the remaining 11 fishes had fed on small cichlid fishes, and six on bottom dèbris (plant tissue) and insects (both adult and larval). Despite a careful search, no remains of Mollusca were identified. Admittedly, 13 specimens do not constitute an adequate sample, but, if 13 Lake Victoria *A. alluaudi* in the same size-range were examined, every specimen with intestinal contents would have yielded remains of Mollusca.

Likewise, in four *A. alluaudi* from Lake Edward and one from Lake George, the predominant food was insects, although three individuals had scanty remains of small Gastropoda in the intestines. The snails could not be identified, except in so far as they were not *Melanoides* sp.

Coloration in life (known only from Lake Victoria). Sexual dimorphism is less marked in this species than in *Haplochromis* and the other monotypic genera. *Females and immature males.* Ground colour golden, overlain with olivaceous green, becoming yellow ventrally; a dark band runs obliquely downwards through the eye and becomes continuous with the lachrymal stripe, which runs obliquely backwards to the anterior tip of the preoperculum; often another dark band along the vertical limb of the preoperculum. All median fins olivaceous-yellow, the dorsal and anal outlined in black; caudal maculate. Pectoral fins hyaline; pelvics faintly yellow or hyaline.

Breeding males. Coloration essentially that of females except that the spinous dorsal is suffused with maroon, as is the entire anal fin, and the soft dorsal is densely spotted with maroon maculae. Anal fin with numerous yellow ocelli arranged in three or four vertical and the same number of horizontal rows. Pelvic fins black, the first ray pearly. Cephalic markings usually more intense than in females.

Preserved material : Adult males. Ground colour greyish-brown to brown, lighter ventrally ; five or six dark transverse bars, often interrupted ventrally, on the flanks ; occasionally an interrupted mid-lateral stripe. Cephalic markings as described above. Soft dorsal fin and entire caudal maculate ; lappets of spinous dorsal, margin of soft dorsal and entire margin of anal fin black. Pelvics black laterally, the first ray pearly. Ocelli on anal fin dark grey. *Females and immature males.* Ground colour as in males but lighter. Soft dorsal and entire caudal weakly maculate or immaculate. Cephalic markings fainter than in males. Anal fin without ocelli, but in some individuals a few, small, light spots occur in the position of the ocelli. Pectoral and pelvic fins hyaline.

Affinities. The relationship of *Astatoreochromis alluaudi* to the other monotypic genera of Lake Victoria and to certain species of *Haplochromis* was discussed above. It only remains to consider Regan's suggestion that *A. alluaudi* is " Near *H. gestri*, especially distinguished by the increased number of dorsal and anal spines and the large blunt pharyngeal teeth ". (*Haplochromis gestri* is a synonym of *H. obesus* (Blgr.) (see p. 182).

With the information now available on the anatomy and ecology of both species, it is clear that *A. alluaudi* and *H. obesus* are not closely related. *Haplochromis obesus* belongs to a group of endemic Lake Victoria species which has developed the highly specialized habit of feeding on the embryos and larvae of other cichlid fishes (p. 187.) *Astatoreochromis*, on the other hand, possesses the potentialities for developing into a highly specialized mollusc-eater, although one subspecies is apparently a generalized bottom feeder. Besides the morphological differences noted by Regan, there are marked dissimilarities in the dentition and jaws of the two species. On the scale of divergence found in the *Haplochromis* and related species occurring in Lake Victoria, *A. a. alluaudi* and *H. obesus* must be placed in very distinct lineages.

Differences in caudal fin length and the form of the pharyngeal bones are sufficiently well-marked to warrant the recognition of two subspecies of *Astatoreochromis*, one occurring in Lakes Victoria and Kyoga (including the Victoria Nile), and the other in Lakes Edward, George, Nakavali and Kachira, and in the Semliki River.

Admittedly one of the characters distinguishing the two groups could be considered a response to environmental differences (see p. 172). On the other hand, the importance of geographical isolation must be recognized. At present, and probably for a considerable period in the past, the western group of Lakes (Edward, Nakavali and Kachira) have been isolated from Lake Victoria by extensive papyrus-swamp divides on the interconnecting river systems (see Worthington, 1932). Likewise, Lakes Kachira and Nakavali are isolated from Lake Edward by intervening papyrus-swamps. Thus, although *Astatoreochromis* is relatively tolerant of papyrus-swamp conditions (see p. 174) the existence of such extensive swamp divides must considerably reduce any gene flow between the different lakes. Unfortunately, there is insufficient material from Lakes Edward, Kachira and Nakavali to determine whether a distinct subspecies occurs in each lake. At present, therefore, only two subspecies can be recognized.

Astatoreochromis alluaudi alluaudi Pellegrin

Diagnosis. *Astatoreochromis a. alluaudi* differs from the other subspecies in having a more massive lower pharyngeal bone with a greater number of molariform teeth, see Text-fig. 3 (ratio of head length to width of lower pharyngeal bone 2·4–3·1, Mean 2·7), and in having a shorter caudal fin (21·4–28·5 [Mean 24·3] per cent of standard length).

Other, ecological differences will be discussed below.

Distribution. Lakes Victoria, Kyoga and the Victoria Nile.

Astatoreochromis alluaudi occidentalis subsp. nov.

Type specimen. A male, 125 + 35·0 mm. long, B.M. (N.H.) Reg. No. 1933.2.23. 146, collected by Worthington from Lake Nakavali.

Diagnosis. Differs from the nominate subspecies in having a finer lower pharyngeal bone with fewer molariform teeth, see Text-fig. 3 (ratio of head length to width of lower pharyngeal bone 2·6–3·6, Mean 3·0) and in having a longer caudal fin (24·0–31·6, Mean 27·2 per cent of standard length).

Distribution. Lakes Edward, George, Nakavali and Kachira ; the Semliki River above the rapids.

Ecology. *Habitat*. *A. a. alluaudi*, unlike the majority of *Haplochromis* species in Lake Victoria, is not confined to any particular type of substrate. Indeed, in this lake the subspecies is ubiquitous in all areas where the water is less than 60 feet deep. There are also indications that in Lake Victoria *A. a. alluaudi* may extend into deeper water. Graham collected one specimen in surface nets set over 193 feet of water some distance off-shore (Station 71 ; 0° 20¾′ S., 33° 1½′ E.; in the collections of E.A.F.R.O. there is one other specimen caught by nets set on the bottom at *ca*. 180 feet (0° 4′ S., 33° 14′ E.).

During rainy seasons, post-larval *A. a. alluaudi* have been found in pools and streams some distance inside papyrus-swamps. Larger young (40–50 mm. S.L.) enter small temporary streams when these are flowing into the lake. Neither the papyrus-swamp habitat nor that of temporary streams is occupied by endemic *Haplochromis* or related species. Young and adults of the widely-distributed, fluviatile-lacustrine species *H. nubilus* (Blgr.) and *H. multicolor* (Schoeller) do, however, live in such habitats.

No habitat data are available for *A. a. alluaudi* in the Victoria Nile and Lake Kyoga, nor for *A. a. occidentalis* in any lake. Specimens of the latter have been collected from the Semliki River near its source in Lake Edward.

Food. *Astatoreochromis a. alluaudi* (Lake Victoria). The stomach and intestinal contents of 40 fishes (48–163 mm. S.L.) from different localities clearly indicate that *A. a. alluaudi* feeds almost exclusively on Mollusca, especially Gastropoda. In most of the specimens examined, some insect larvae were also found ; but, both in volume and numbers, these represented only a small fraction of the ingested material. The very fragmentary nature of the shells found in the alimentary tract precluded accurate identification of the mollusc species eaten. However, it seems most probable that the principal gastropod prey is *Melanoides tuberculata* (Müller), and the chief lamellibranch, *Corbicula* sp.

Astatoreochromis a. occidentalis. Lake Nakavali. Thirteen specimens 50–137 mm. S.L. were examined ; two were empty. In the largest fish, the entire alimentary tract was filled with plant debris ; five specimens (79–123 mm. S.L.) each contained fragmentary remains of small cichlid fishes (probably *Haplochromis*), with, in two, a little plant debris and some insect remains. The five smaller fishes (50–72 mm.) contained fragmentary insect remains (especially larval and adult Diptera) and plant debris.

Lake Edward. Only four specimens (62–76 mm. S.L.) were available for gut analysis ; three contained a few unidentifiable fragments of mollusc shells together with bottom debris and the fourth (71 mm. S.L.), mostly adult insects (Diptera) and the very fragmentary remains of a small fish. Although the mollusc fragments could not be identified positively they were not derived from *Melanoides*.

Lake George. The alimentary tract of the single fish available (80 mm. S.L.) contained fragments of adult insects.

Lake Kachira. The three specimens examined (66–78 mm. S.L.) were all from one station and contained only bottom debris and plant remains (including water-lily seeds) ; a few fragments of insects were found in the intestine of one individual.

Breeding. Both subspecies of *Astatoreochromis alluaudi* are female mouth-brooders; exact spawning sites are not known. In Lake Victoria, males of *A. a. alluaudi* less than 100 mm. S.L. are immature but females are mature at about 95 mm. S.L. The three specimens of *A. a. occidentalis* from Lake Kachira (66–78 mm. S.L. 1 ♂ and 2 ♀) are all sexually active, thus suggesting that in this lake the subspecies reaches maturity at a smaller size than *A. a. alluaudi* in Lake Victoria. Little information was obtained on the size of sexually mature *A. a. occidentalis* in other lakes ; a brooding female 57 mm. S.L. from Lake Nakavali and a ripe female 62 mm. long from Lake Edward seem to indicate that in these lakes female *A. a. occidentalis* also mature at a smaller size than do the females of *A. a. alluaudi* in Lake Victoria. It is possible that differences in the feeding habits of the two subspecies may be primarily responsible for the smaller adult size of *A. a. occidentalis*.

A marked disparity was noticed in the sex ratio of *A. a. alluaudi* from Lake Victoria and *A. a. occidentalis* from Lake Nakavali ; there is insufficient material to determine the sex ratio in other localities. Using only those specimens whose sex could be ascertained with certainty, the ratio is 16 ♀ : 46 ♂ in Lake Victoria, and 1 ♀ : 7 ♂ in Lake Nakavali. Reasons for this discrepancy are obscure but at least any bias introduced by collectors selecting brightly coloured males can be discounted ; both sexes are remarkably similar in colour. Furthermore, collections from Lake Victoria were made so as to eliminate this bias.

SUMMARY

1. The monotypic genus *Astatoreochromis alluaudi* is redescribed.

2. The generic characters are discussed, particularly from the phylogenetic viewpoint. It is thought that *A. a. alluaudi* was not derived from the same stem as other

Victoria and Edward species with hypertrophied pharyngeal bones and teeth. By the same tokens, *Astatoreochromis* is not closely related to the other and endemic monotypic genera of the two lakes. The genus is apparently related to such fluviatile species as *Haplochromis vanderhorsti* (Malagarasi River system) and *H. straeleni* (Congo system).

3. Two subspecific groups may be recognized, one from the Lake Victoria system and the other from lakes in western Uganda. These groups are given subspecific status, namely: *Astatoreochromis a. alluaudi* from Lakes Victoria and Kyoga, and the Victoria Nile; and *A. a. occidentalis* from Lakes Edward, George, Nakavali and Kachira, and the Semliki River.

4. The feeding habits of the two subspecies are described.

Study Material and Distribution Records.

Astatoreochromis a. alluaudi

Museum and Reg. No.	Locality	Collector
	Kenya	
Paris Museum		
04,137 (Lectotype)	Kavirondo Bay	Alluaud
04,138–9 (Paratypes)	,, ,,	,,
B.M. (N.H.).—1904.6.281 (Paratype, presented by Paris Museum)	,, ,,	,,
B.M. (N.H.).—1958.7.9.2	Kisumu Harbour	E.A.F.R.O.
	Uganda	
B.M. (N.H.).—1906.5.30.506–9	Entebbe	Degen
,, 1906.5.30.505	Bunjako	,,
,, 1907.5.7.73–76	Buddu Coast	Simon
,, 1911.3.3.112–3113	Jinja, Ripon Falls	Bayon
,, 1958.7.9.3–5	Grant Bay	E.A.F.R.O.
,, 1958.7.9.6	Karinya (near Jinja)	,,
,, 1958.7.9.7–16	Jinja	,,
,, 1958.7.9.18–21	Pilkington Bay	,,
,, 1958.7.9.22	Thruston Bay	,,
,, 1958.7.9.23	0° 4′ S., 33° 14′ E.	,,
,, 1958.7.9.24–37	Entebbe Harbour	,,
,, 1958.7.9.38	Beach nr. Nasu Point	,,
,, 1958.7.9.39–40	Stream at Bugungu, Napoleon Gulf	,,
,, 1958.7.9.50	Ekunu Bay	,,
,, 1958.7.9.51–58	Ramafuta Island	,,
	Tanganyika	
,, 1958.7.9.1	Mwanza	,,
,, 1958.7.9.17	Majita	,,
,, 1958.7.9.41–49	Godziba Is.	,,
	Lake Victoria, Locality Unknown	
,, 1908.5.19.51	—	D. Radcliffe
,, 1928.5.24.370–372	—	M. Graham

Museum and Reg. No.	Locality	Collector
	Lake Kyoga and the Victoria Nile	
,, 1911.3.27.21	Between Lake Kyoga and the Murchison Falls	F. Melland
,, 1911.3.3.108	Bululo, Lake Kyoga	Bayon
,, 1911.3.3.109–110	Kakindu, Victoria Nile	,,
	Astatoreochromis a. occidentalis	
	Lake Kachira	
B.M. (N.H.).—1933.2.23.160–162		E. B. Worthington
	Lake Edward	
,, 1933.2.23.137–140		,,
	Lake George	
,, 1933.2.23.141		,,
	Lake Nakavali	
,, 1933.2.23.142–159		,,

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A REVISION OF THE LAKE VICTORIA *HAPLOCHROMIS* SPECIES (PISCES, CICHLIDAE), PART III

By P. H. GREENWOOD
British Museum (Natural History) London

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INTRODUCTION

FIVE of the seven species described in the first part of this paper are known to feed almost exclusively on the embryos and larvae of other cichlid fishes, especially *Haplochromis*. Data on the food of the sixth species are very inadequate but are nevertheless indicative of similar habits. The seventh species is known from only a few specimens, but various morphological similarities between it and two other species of this group suggest embryo and larval fish-eating habits.

If the species on which these fishes prey are mouth-brooders, it can be said that none of the young found in the stomachs of the predators was of a size at which it would normally have left the parental mouth.

Despite identical feeding habits, the members of this species group are morphologically heterogeneous and exhibit convergence only in a tendency for the teeth to be deeply embedded in the oral mucosa and in having capacious mouths. Furthermore, in most species there is a marked intra-specific variability in gross morphology, especially of the head. It seems that the group is of polyphyletic origin.

The four species dealt with in the second part of the paper are, morphologically speaking, somewhat isolated from the other *Haplochromis* of Lake Victoria. All are insectivores.

Haplochromis cronus sp. nov.

(Text-fig. 1)

Holotype. A female, 135 mm. standard length, from Buka Bay, Uganda.

Description, based on eight specimens, including the holotype, 114–135 mm. standard length.

Depth of body 39·5–43·5 per cent of standard length, length of head 30·3–34·6 per cent. Dorsal head profile strongly curved, with a well-defined but localized swelling above the anterior part of the eye. Preorbital depth 16·7–18·2, mean (M) 17·5 per cent of head length; least interorbital width 31·9–35·5 (M = 33·1) per cent. Snout slightly broader than long, its length 31·6–35·7 (M = 33·7) per cent of head; eye diameter 23·1–26·3 (M = 25·2), depth of cheek 29·3–34·2 (M = 30·1) per cent.

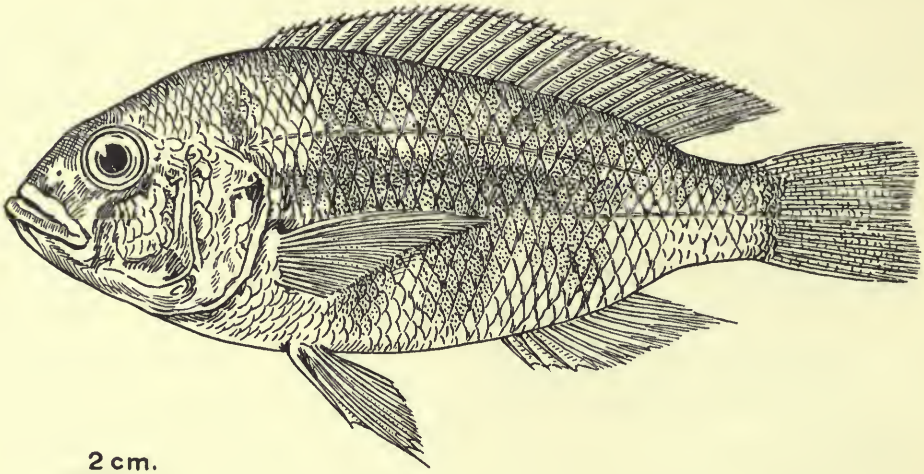

FIG. 1. *Haplochromis cronus;* holotype. Drawn by Miss D. Fitchew.

Caudal peduncle 15·2–17·3 per cent of standard length, 1·1–1·3 (mode 1·3) times as long as deep.

Jaws equal anteriorly; lips thickened; posterior tip of the maxilla not bullate and almost completely hidden beneath the preorbital, extending to the vertical through the anterior part of the eye. Lower jaw stout and deep, its length 29·3–34·2 (M = 30·1) per cent of the head, 1·2–1·4 times as long as broad.

Gill rakers stout; 8–10 on the lower limb of the first arch.

Scales ctenoid; lateral line with 32 (f.5), 33 (f.1) or 34 (f.2) scales. Cheek with four or five series. Five to 8 scales between the dorsal fin origin and the lateral line; 8 or 9 between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.7) or 25 (f.1) rays, anal (damaged in one specimen) with 12 (f.7), comprising XV or XVI, 9–10 and III, 9 spinous and branched rays for the fins respectively. Pectoral fin shorter than the head ; pelvic fins with the first soft ray produced and extending to the vent in females and to the anal fin in males. Caudal truncate, the rays noticeably coarse ; densely scaled over about four-fifths of its length (a most unusual character in Lake Victoria *Haplochromis* species).

Teeth. The outer row in both jaws is composed of unicuspid, fairly stout teeth, implanted vertically and not hidden by thickened oral mucosa ; there are 40–56 teeth in this series of the upper jaw. The inner teeth are small and unicuspid, arranged in two rows (three in one specimen) in both jaws, and are separated from the outer series by a distinct space.

Lower pharyngeal bone triangular, the dentigerous area about 1·3 times as broad as long ; the teeth are slender and cuspidate.

Syncranium. The syncranium is noticeable for its short and deep neurocranium (comparable with *H. obesus* ; see p. 185) and for the stout but otherwise unspecialized dentary. These characters were determined from a radiograph B.M. (N.H.) Reg. No. 957 and the partial dissection of one specimen.

Vertebrae : 13 + 16 in the single specimen radiographed.

Coloration of preserved material : Adult females and sexually quiescent males. Ground colour dark golden above, lighter below, with traces of a golden-yellow flush on the operculum : a broad, mid-lateral stripe of variable depth and intensity crossed by four or five broad but faint transverse bars on the flanks ; a well-defined lachrymal stripe. Dorsal fin hyaline, with dark spots and bars on the soft part (probably deep red in life) ; caudal hyaline (densely maculate in males) ; proximal two-thirds of anal fin dark, remainder light ; pelvic fins dark (black laterally in males).

One of the three females available has a typical "*bicolor*" (piebald black and yellow) coloration, similar to that described in several other and apparently unrelated *Haplochromis* species and in two monotypic genera (Greenwood, 1957, and p. 213).

Sexually active male. Dark brown above, sooty-grey below ; transverse and lateral stripes faint except at their junction mid-laterally. Dorsal fin dusky, the soft part maculate ; caudal dusky and densely maculate ; anal dark, except for its extreme tip and two colourless ocelli. Pelvic fins black on the lateral half and dusky mesially.

Distribution. Known only from Lake Victoria.

Ecology : Habitat. Five of the eight specimens are from an exposed beach habitat, one is from the sandy littoral of a sheltered gulf, one from the mud-bottom sublittoral of a sheltered bay and one from shallow water near a reed bed (no other data available). In no locality was the water more than 20 feet deep.

Food. Four specimens contained food in the stomach ; in each, only larval cichlid fishes were found (in three fishes these were identified as *Haplochromis*) ; the number of larvae in each fish was : 127 (*ca.* 11 mm. long) ; 50 (*ca.* 11 mm.) and 41 (*ca.* 11 mm.). The remains found in the fourth fish were too fragmentary to allow even an estimate of numbers.

Breeding. Two females were found with, in one, larvae and in the other, newly hatched embryos in the buccal cavity. Since the ovarian condition of these fishes was clearly " spent " it can be assumed that the young were the fishes' own brood and not prey.

Affinities. Haplochromis cronus belongs to the small group of deep-bodied, broad-headed *Haplochromis* whose adult size is *ca.* 100–140 mm. S.L. The specialized mollusc-eating species *H. pharyngomylus* Trewavas and *H. ishmaeli* Boulenger may be cited as examples of this morphotype. *H. cronus* differs from all other members of the group in having a densely and extensively scaled caudal fin. The species shows some affinity with *H. obesus* and *H. maxillaris,* forms which may have evolved independently from an *H. cronus*-like ancestor.

Diagnosis. From other species with a similar gross morphology, *H. cronus* can be distinguished, primarily, by its almost completely scaled caudal fin (four-fifths scaled in *H. cronus* cf. two-thirds scaled in other species). The relatively large, completely exposed, caniniform and recurved teeth of *H. cronus,* together with an unmodified lower pharyngeal dentition and the presence of a supra-orbital swelling, also serve to distinguish *H. cronus* from other morphologically similar species.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1958.1.16.85 (Holotype)	Buka Bay	E.A.F.R.O.
B.M. (N.H.).—1958.1.16.86–89	,, ,,	,,
,, 1958.1.16.90	Napoleon Gulf near Jinja	,,
,, 1958.1.16.91	Pilkington Bay	,,
	Kenya	
,, 1928.5.24.408	Port Victoria (Graham's St. No. 84)	M. Graham

Haplochromis obesus (Boulenger) 1906

(Text-figs. 2 and 3)

Pelmatochromis obesus (part) Boulenger, 1906, *Ann. Mag. nat. Hist.* (17) **17**, 447 (type specimen, by restriction [specimen figured in *Fish. Nile*], only) ; *Idem*, 1907, *Fish. Nile*, 491, pl. LXXXIX fig. 5 ; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 414, fig. 283.
Lipochromis obesus (Boulenger), Regan, 1920, *Ann. Mag. nat. Hist.* (9) **5**, 45 (foot-note).
Haplochromis obesus (Boulenger), Regan, 1922, *Proc. zool. Soc. London*, 170.
Paratilapia gestri Boulenger, 1911, *Ann. Mus. Genova* (3), **5**, 67, pl. I, fig. 3.
Paratilapia gestri (part, holotype only). Boulenger, 1915, *Cat. Afr. Fish.* **3**, 318, fig. 211.
Haplochromis gestri (part, holotype of *P. gestri* only), Regan, 1922, *Proc. zool. Soc. London*, 170.

The union of *H. obesus* and *H. gestri* might be questioned if only the type specimens of the two species were available ; indeed, for a long time I thought that the species were distinct. However, after examining a large series of *H. gestri*-like specimens, I am forced to conclude that the type and unique specimen of *H. obesus* is merely an aberrant individual from a species whose modal morphotype is " *gestri* "-like.

In my opinion, the critical specific character-complex is the broad and stout lower jaw, combined with a relatively fine premaxilla and a stout, posteriorly bullate maxilla. These characters are easily verified in the type specimens of *H. obesus* and *H. gestri*, and have been further confirmed in a radiograph of the former.

In its gross morphology and partly in its physiognomy, the type of *H. obesus* differs from all except one of the 46 specimens now referred to this species ; these differences may be partly attributable to *post-mortem* changes and poor preservation. In Boulenger's figure (reproduced here as Text-fig. 2) the mouth is shown as it appeared when closed artifically, with the result that the gape is very oblique. With the passage of time, the specimen has softened and it is now possible to close the mouth more easily. If this is done, it will be seen that the angle of the mouth is only slightly oblique and that the dorsal head profile, although sloping steeply, is not so markedly concave as it appears in the figure. The lower jaw closes within the upper and only the anterior part of the maxilla is covered by the preorbital. Whether or not this is due to a natural deformity or to *post-mortem* distortion, I cannot say.

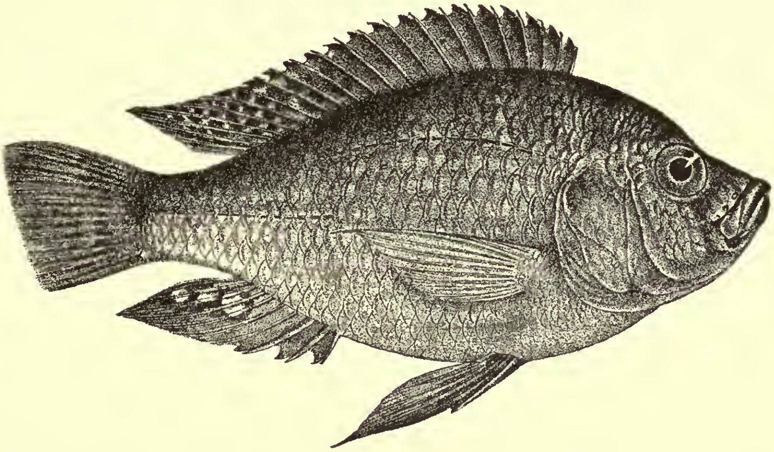

FIG. 2. *Haplochromis obesus ;* holotype (from Boulenger, *Fishes of the Nile*).

Although, in appearance, the majority of specimens resemble the holotype of *H. gestri*, there are several others which depart from that mode but still retain the diagnostic dentary, upper jaw elements and dentition of the species.

Description, based on 48 fishes (71–170 mm. S.L.) including the type, and the holotype of *H. gestri*.

Depth of body 33·6–47·3 per cent of standard length ; length of head 30·3–35·9 per cent. Physiognomy variable, the dorsal head profile straight or very slightly concave in the interorbital region, sloping steeply (Text-fig. 4) ; most fishes resemble the figured specimen. Preorbital depth 12·5–17·3 (M = 15·4) per cent of head length, least interorbital width 27·3–37·0 (M = 32·2) per cent. Snout 1·20–1·33 times as broad as long, its length 28·0–39·5 (M = 33·5) per cent of head ; eye diameter shows negative allometry with standard length, being 23·7–30·4 (M = 27·6) per cent in

23 fishes less than 125 mm. S.L. and 20·5–27·9 (M = 23·6) per cent in 25 larger individuals; depth of cheek 21·8–31·8 (M = 27·6) per cent.

Caudal peduncle 12·8–17·9 per cent of standard length, its length 1·0–1·6 (modal range 1·0–1·2) times its depth.

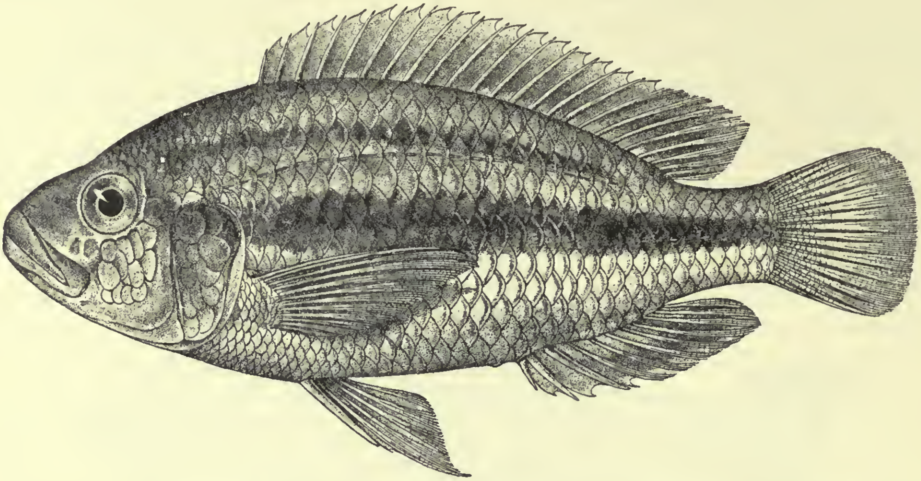

FIG. 3. *Haplochromis obesus;* typical form (holotype of *Paratilapia gestri*). From Boulenger, *Ann. Mus. Genova*, 1911.

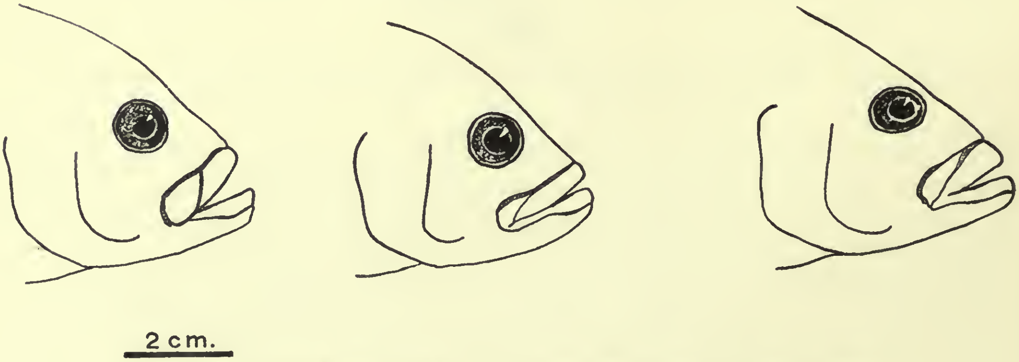

FIG. 4. *Haplochromis obesus;* individual variability of head profile.

Mouth slightly oblique, maxilla bullate posteriorly and only partly covered by the preorbital, reaching the vertical through some part of anterior half of eye. Lips somewhat thickened; jaws equal anteriorly, the length of the lower showing a positive but widely scattered allometry with standard length, 40·0–54·5 per cent of head length. Length/breadth ratio of the lower jaw 1·0–1·6 (mode 1·3).

Gill rakers short and stout, 9 or 10 (rarely 8 or 11) on the lower part of the first arch.

Scales ctenoid ; lateral line with 29 (f.1), 31 (f.11), 32 (f.18), 33 (f.15) or 34 (f.2) scales ; cheek with 3 or 4 (rarely 2) series. Six or 7 (rarely 8) scales between the dorsal fin origin and the lateral line ; 6–8 between pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.21), 25 (f.26) or 26 (f.1) rays, anal with 10 (f.2), 11 (f.23), 12 (f.21) or 13 (f.1), comprising XV–XVI (rarely XVII), 8–10 and III, 8 or 9 (rarely 10) spinous and branched rays for the fins respectively. Pectoral shorter than the head. Pelvic fins with the first soft ray produced, more particularly so in adult males. Caudal subtruncate or less commonly, obliquely truncate.

Teeth. Both the inner and outer series of teeth are deeply embedded in the oral mucosa, so that only the tips protrude.

Except for the smallest specimens, the outer teeth in both jaws are relatively stout and unicuspid with conical crowns. In small specimens most teeth are unequally bicuspid, or there may be an admixture of uni- and bicuspid forms. There are 34–52 teeth in the outer series of the upper jaw.

The shape of the teeth is variable ; in most specimens the anterior and some lateral outer teeth in the lower jaw have the crown bent so that its tip is directed anteriorly. In the upper jaw there is an admixture of such teeth with the more usual recurved and conical types. Teeth with anteriorly directed crowns are known only in *H. obesus*, *H. maxillaris* and *H. melanopterus*.

The inner teeth are unicuspid and slenderly conical in fishes over 100 mm. S.L.; in smaller individuals there is a combination of unicuspid and weakly tricuspid teeth. Anteriorly in both jaws the inner teeth are arranged in one or, less commonly, two series ; the interspace between inner and outer teeth is greatly reduced or even absent.

Lower pharyngeal bone short and broad, the dentigerous surface 1·2–1·6 times as broad as long ; pharyngeal teeth cuspidate and laterally compressed.

Syncranium. The most outstanding skeletal characteristic of *H. obesus* is the broad and stout lower jaw (Text-fig. 5A). The "*obesus*"-type dentary is unique amongst the *Haplochromis* of Lake Victoria. When compared with one of the larger but generalized species the dentary of *H. obesus* is noticeably bullate in the region where each ramus divides into ascending and horizontal rami.

Departure from a generalized *Haplochromis* condition is also seen in the maxilla, which is deeper and more bullate posteriorly. The neurocranium closely resembles that of *Hoplotilapia retrodens* Hilgendorf and *Platytaeniodus degeni* Boulenger, since the preorbital face is short and the supra-occipital crest deep (Greenwood, 1956). This intergeneric convergence is probably associated with the relatively massive lower jaw of all three species.

When compared with other *Haplochromis* (e.g. *H. cronus* and *H. pharyngomylus*) having approximately the same adult size and similar body-form, it is obvious that the mouth of *H. obesus* is more distensible and more protrusible. These factors may be associated with the specialized feeding habits of the species (see p. 204).

Vertebrae : 13 + 16 and 13 + 15 (type *H. obesus*).

Coloration in life : Adult males. Ground colour dark malachite green shading to silvery-blue ventrally ; a coppery sheen on the operculum, chest and belly ; a distinct dark mid-lateral stripe. Dorsal fin dark, with an overall pinkish flush; caudal and anal fins dark, the latter with four or five orange-yellow ocelli arranged in one or, more frequently, two rows. Sexually quiescent males have a similar but less intense coloration. *Adult females.* Olivaceous-silver shading to silver ventrally; a distinct, dark mid-lateral stripe. All fins hyaline; in some individuals there are small yellow spots in the position of the anal ocelli in males. Some females show a typical "*bicolor*" black and silver (or yellow) piebald coloration. No estimate of the frequency of "*bicolor*" individuals can be made from the data available; such females have, so far, only been found in the Napoleon Gulf, near Jinja, Uganda.

A second atypical colour-form is also known. Fishes showing the extreme expression of this coloration are uniformly black, but lighter (sooty) ventral coloration is more usual. Unlike the "*bicolor*" pattern, the dark form is not sex-limited and is known to occur in several different areas of the lake. Furthermore, it shows some intergradation with the usual coloration, at least in males.

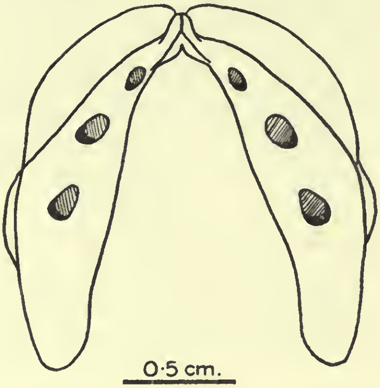

FIG. 5 (A). *Haplochromis obesus*; outline of dentary, ventral view.

Colour in preserved material: Both sexes. Ground colour golden to dark brown (adult males generally darkest); a well defined, dark, mid-lateral stripe and an ill-defined dorsal stripe following the contour of the upper lateral-line; 5–9 vertical bars on the flanks and caudal peduncle; often faint indications of a lachrymal stripe. Pelvic fins black in adult males, otherwise colourless, as are all other fins; soft dorsal and the entire caudal weakly maculate.

Distribution. Lake Victoria and Lake Kwania (Kyoga system).

Ecology: Habitat. Haplochromis obesus is apparently restricted to water less than 50 feet deep in the littoral and sublittoral zones of Lake Victoria. Most of the specimens were caught over a hard substrate (sand, shingle or rock) but two were caught over a soft mud bottom. In all probability, the distribution of *H. obesus* is closely linked with the spawning and brooding areas of the cichlid fishes on whose embryos and larvae it preys.

Food. Of the 73 specimens examined, 18 had food in the stomach. In every one of these fishes, only fish embryos or larvae were found ; with one exception (a small cyprinid fish) the prey could be identified as Cichlidae. A hundred embryos at the same stage of development were recorded from one stomach and in many others the embryos or larvae were all at the same developmental stage ; embryos at different ontogenetic stages were, however found in some individuals.

The possibility that these stomach contents did not represent food but rather the fishes' own young accidently swallowed, can be overruled by the following considerations : a mixture of early and advanced ontogenetic stages was found in one stomach ; embryos and larvae were found in the stomachs of both male and female fishes and it is unknown amongst the Lake Victoria cichlids for both parents to share brooding duties ; early embryos were identified in the stomach contents of an immature female ; and finally, personal observations show that it is unusual for a brooding female to swallow her brood when she is captured ; generally, the young are jettisoned.

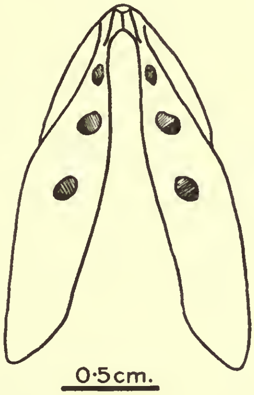

FIG. 5 (B). *Haplochromis parvidens ;* outline of dentary, ventral view.

It is not known how *H. obesus* or the other larval fish-eating species obtain their prey. The question is complicated because the principal source of food for these species is the young of other cichlid fishes. Both species of *Tilapia* in Lake Victoria and all species of *Haplochromis* whose breeding habits are known are female mouth-brooders. Although late larval cichlids do leave the parental mouth, the earlier, non-free-swimming stages do not, except when the parent is so harrassed that it jettisons the brood. Unless a number of *Haplochromis* are not mouth-brooders, it seems that the larval and embryo fish-eating species employ some means of forcing the parent fish to abandon its brood. It may be added that there is no evidence to indicate that any Lake Victoria *Haplochromis* are not mouth-brooders.

Breeding. A single brooding female was recorded : young removed from the buccal cavity were in the germ-ring stage of development. There is no sex-correlated size difference in adult fishes and sexual maturity is reached at a standard length of about 85 mm.

Affinities. Regan (1922) suggested that *H. gestri* (= *H. obesus*) was near *Astatoreochromis alluaudi* Pellegrin. With the additional information now available on both species, this opinion is no longer tenable. *A. alluaudi* is a specialized mollusc-eater with hypertrophied pharyngeal bones and the consequent modifications to the syncranial architecture (see Greenwood, 1954). Although *H. obesus* has a markedly modified lower jaw and somewhat atypical upper jaw features, it is more closely related to the generalized *Haplochromis* species. The relationships of *A. alluaudi* lie, apparently, with some of the semi-specialized fluviatile *Haplochromis* of the Malagarasi and Congo rivers (Greenwood op. cit. and p. 167). Any resemblance between *A. alluaudi* and *H. obesus* is entirely superficial and attributable to the stout bodies and broad heads of the two species.

Perhaps the closest relatives of *H. obesus* are *H. cronus* and *H. maxillaris*, with which species it not only shows certain similarity in gross and detailed morphology, but it also shares the same food requirements.

Diagnosis. The shape of the lower jaw (in which there is usually a predominance of unicuspid outer teeth with anteriorly directed crowns) is the most trenchantly diagnostic character. The deeply embedded teeth, together with certain morphometric characters of the head, serve to distinguish *H. obesus* from other Lake Victoria *Haplochromis* species.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.311 (Holotype *Pelmatochromis obesus*)	Bunjako	Degen.
Genoa Museum (Holotype *Paratilapia gestri*)	Jinja	Bayon.
B.M. (N.H.).—1958.1.16.140	Ekunu Bay	E.A.F.R.O.
,, 1958.1.16.141	Buka Bay	,,
,, 1958.1.16.142	Channel between Yempita and Busiri Isles, Buvuma Channel	,,
,, 1958.1.16.143–150	Beach near Nasu Point, Buvuma Channel	,,
,, 1958.1.16.154–156	SE. tip of Ramafuta Is., Buvuma Channel	,,
,, 1958.1.16.157	Karinya, Napoleon Gulf	,,
,, 1958.1.16.158–161	Entebbe Harbour	,,
	Kenya	
,, 1958.1.16.151–153	Kisumu Harbour	,,
	Lake Victoria, Locality Unknown	
,, 1958.1.16.162–164	—	,,
,, 1928.5.24.341–2	—	M. Graham.
	Lake Kwania	
,, 1929.1.24.509	—	E. B. Worthington.

Haplochromis maxillaris Trewavas, 1928
(Text-fig. 6)

Pelmatochromis microdon (part) Boulenger, 1906, *Ann. Mag. nat. Hist.* (7) **17**, 441 ; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 412.
Haplochromis microdon (Boulenger), (part), Regan, 1922, *Proc. zool. Soc. London*, 173.
Haplochromis maxillaris Trewavas, 1928, *Ann. Mag. nat. Hist.* (10) **2**, 94.

Lectotype. A male 114 mm. standard length (B.M. (N.H.) Reg. No. 1928.5.24.486) from Emin Pasha Gulf, Tanganyika Territory (2° 31½′ S., 31° 43½′ E.), Michael Graham's station 227.

Description, based on 58 specimens (including the types) 90–160 mm. S.L.

Depth of body 32·0–42·8 per cent of standard length, length of head 30·0–34·8 per cent. Physiognomy variable, its shape partly dependent on the angle of the mouth and whether the lower jaw protrudes or not ; dorsal head profile concave (markedly so in a few specimens) and sloping at an angle of 40°–50°. A few specimens bear a superficial resemblance to *H. obesus*, but despite this variability in gross morphology there is a distinct modal specific facies (see Text-fig. 6).

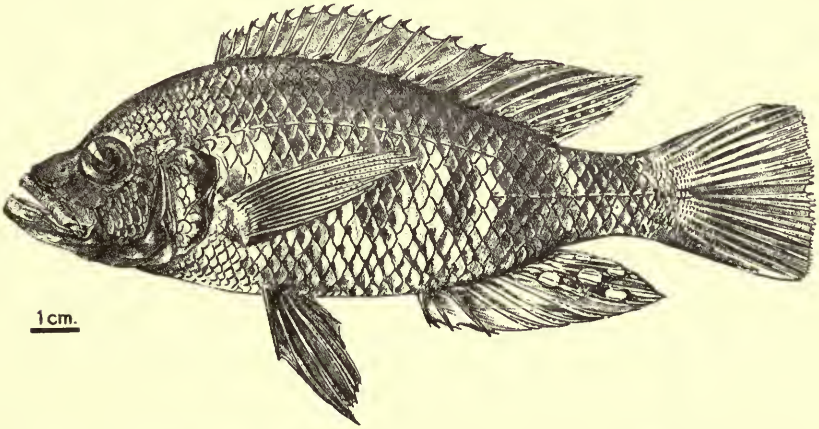

FIG. 6. *Haplochromis maxillaris ;* holotype. Drawn by Miss M. Fasken.

Preorbital depth 11·4–16·3 (M = 13·9) per cent of head length, least interorbital width 22·6–31·3 (M = 26·5) per cent. Snout slightly broader than long, rarely as long as broad, its length 25·8–34·0 (M = 30·3) per cent of head. Eye diameter shows negative allometry with standard length : in 15 fishes 60–100 mm. S.L. it is 30·0–38·0 (M = 33·2) per cent of head and in 43 larger individuals it is 25·0–31·4 (M = 27·3) per cent. Depth of cheek positively allometric with standard length : for the two size groups as above, 18·8–24·2 (M = 20·7) and 21·6–27·8 (M = 26·4) per cent head length.

Caudal peduncle 12·6–18·5 per cent of standard length, 1·1–1·7 (modal range 1·2–1·3) times as long as deep.

Mouth distensible and usually somewhat oblique when closed, but horizontal in a few specimens. Maxilla partially hidden by the preorbital, its posterior tip bullate and reaching the vertical to the anterior part of the eye or even as far as the pupil. Lips thickened. Lower jaw usually projecting, but in a few fishes the jaws are equal anteriorly. Length of lower jaw shows positive allometry with standard length, in fishes 60–100 mm. S.L. it is 39·0–47·5 (M = 44·8) per cent of head length, and in larger fishes 46·5–56·0 (M = 50·0) per cent. Breadth of lower jaw contained 1·3–2·2 (modal range 1·5–1·8) times in its length.

Gill rakers short, 10 or 11 (rarely 9 or 12) on the lower part of the first gill-arch, the lower one or two rakers often greatly reduced.

Scales ctenoid : lateral line with 29 (f.2), 30 (f.7), 31 (f.22), 32 (f.20), 33 (f.4) or 34 (f.1) scales ; cheek with 2 or 3 series ; 5½–7 scales between the dorsal fin origin and the lateral line, 5–7 (rarely 8) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.19), 25 (f.36) or 26 (f.3) rays, anal with 11 (f.18), 12 (f.37) or 13 (f.1), comprising XV–XVI (rarely XVII), 8–10 and III, 8 or 9 (rarely 10) spinous and branched rays for the fins respectively. Pectoral shorter than the head. First soft ray of the pelvic fin produced, extending to the vent in females and to the soft part of the anal fin in adult males.

Teeth. The inner and outer rows of teeth in both jaws are deeply embedded in the thickened oral mucosa ; in many specimens the inner series are invisible without dissection. Furthermore, the outer teeth of the upper jaw are covered by the thickened and inwardly curved margin of the lip.

Fishes less than 80 mm. S.L. have small, weakly and unequally bicuspid outer teeth in both jaws. In larger fishes these teeth are also small, but stout and conical ; those in the upper jaw are recurved, whilst those in the lower jaw generally have the crown curved anteriorly or outwardly. Similar teeth are found in *H. obesus*, but are not the predominant form in that species.

In the three skeletons examined there were 34, 36 and 40 outer teeth in the premaxilla.

The inner teeth are weakly tricuspid in small fishes and unicuspid in larger individuals ; arranged in one or, rarely, two series and separated from the outer row by a small interspace. Inner teeth in the upper jaw are slightly recurved and implanted so as to slope posteriorly ; those of the lower jaw are vertical or directed anteriorly.

Lower pharyngeal bone triangular, the dentigerous area 1·0–1·4 times as broad as long ; teeth slender and cuspidate, those of the two median rows sometimes coarser.

Syncranium. The dentary of *H. maxillaris* departs slightly from the generalized type. As in the dentary of *H. obesus* there is a pronounced lateral bullation of the area surrounding the bifurcation into ascending and horizontal rami.

The premaxilla and maxilla are similar to those of *H. obesus*, except that the premaxillary teeth are restricted to the anterior and antero-lateral areas of the bone. The neurocranium is of a generalized *Haplochromis* type.

Vertebrae : 13 + 16 and 12 + 16 in two skeletons.

Coloration in life : Adult males. Ground colour dark blue-grey, lighter ventrally, with faint indications of darker transverse bars on the flanks. Dorsal fin dusky, with maroon spots between the rays of the soft part; lappets orange-red. Caudal and anal fins smoky-grey, the latter with three to five yellow ocelli arranged in either one or two rows. Pelvic fins dusky. Coloration in life of *immature males* unknown. *Females.* Silver-grey ground colour. Dorsal fin greyish; anal and caudal fins similar but with a yellowish flush and, on the caudal, ill-defined, dark spots. Pelvic fins very faint yellow. Several dark, but faint, transverse bars may appear on the flanks immediately after death.

Colour of preserved material: Males. Dark, some with an underlying silvery ground colour, others almost black. Seven or more transverse bands are sometimes visible on the flanks. Dorsal and caudal fins hyaline and maculate, or dusky; anal hyaline or dusky. Pelvic fins black. *Females.* Ground colour yellowish-silver to brown; some with seven or more transverse bars. All fins hyaline or somewhat dusky; anal and caudal weakly maculate.

Distribution. Known only from Lake Victoria.

Ecology: Habitat. Haplochromis maxillaris is apparently restricted to water less than 30 feet deep, and particularly to the littoral and sublittoral zones of the lake. Most specimens were caught over a hard substrate (sand or shingle), but a few were recorded from mud substrates. Thus the habitat preferences of *H. maxillaris* are almost identical with those of *H. obesus*, the two species frequently being caught in the same gear.

Food. Forty of the 118 individuals examined had identifiable food in the stomach. The smallest specimen (44 mm. S.L.) proved exceptional in that the stomach was filled with Copepoda and blue-green algae. All the remaining 39 fishes had eaten cichlid embryos or larvae. In some individuals, the entire stomach contents were of prey at uniform developmental stage, whilst in other fishes two or more stages (often as widely different as early cleavage embryos and late larval fishes) were present. Both sexes were represented amongst the fishes examined, which came from numerous localities.

The remarkable similarity between the food of *H. maxillaris* and that of *H. obesus* is noteworthy. Again, it is difficult to imagine how the food is obtained if the species preys on mouth-brooding cichlids.

Breeding. There is no information on any aspect of breeding behaviour in this species. All fishes below 100 mm. S.L. were immature; it seems probable that sexual maturity is reached at a length of about 105 mm. Males and females attain the same adult size.

Affinities. The distensible mouth, stout and posteriorly bullate maxilla, and the thickened lips of *H. maxillaris* all suggest affinity with *H. obesus*. Furthermore, conical outer teeth in which the crown is directed anteriorly or laterally are known only in these two species (and *H. melanopterus*, see below, p. 194). Certain specimens of both species show convergence in gross morphology, but the characteristic lower jaw of *H. obesus* usually allows for immediate identification. Apart from these few convergent individuals, the two species differ in certain morphometric details of the head and each has a distinctive modal facies. It is difficult to assess the phyletic significance of the resemblances and differences between *H. obesus* and *H. maxillaris*. The species could be equally well derived from a common stem or from unrelated ancestors within the Lake Victoria species flock.

Study material and distribution records

Museum and Reg. No.		Locality	Collector
		Tanganyika	
B.M. (N.H.).—1928.5.24.486 (Lectotype, *H. maxillaris*)		Emin Pasha Gulf	M. Graham.
,,	1958.1.16.182–184	Majita	E.A.F.R.O.
,,	1958.1.16.188	Mwanza, Capri Bay	,,
		Uganda	
,,	1958.1.16.165–171	Beach near Nasu Point, Buvuma Channel	,,
,,	1958.1.16.172–179	Ramafuta Is., Buvuma Channel	,,
,,	1958.1.16.180	Njoga, Williams Bay	,,
,,	1958.1.16.181	Buka Bay	,,
,,	1958.1.16.185–187	Beach near Hannington Bay	,,
,,	1958.1.16.189	Pilkington Bay	,,
,,	1958.1.16.190–193	Bukafu Bay	,,
,,	1958.1.16.194–198	Entebbe Harbour	,,
,,	1906.5.30.310	Entebbe	Degen.
,,	1958.1.16.199	Ekunu Bay	E.A.F.R.O.
,,	1958.1.16.205–214	Napoleon Gulf, near Jinja	,,
		Kenya	
,,	1958.1.16.200–204	Kisumu Harbour	,,
		Lake Victoria, Locality Unknown	
,, (Syntypes, *H. maxillaris*)	1928.5.24.480–485	—	M. Graham.

Haplochromis melanopterus Trewavas 1928
(Text-fig. 7)

H. melanopterus Trewavas, 1928, *Ann. Mag. nat. Hist.* (10) **2**, 94.

Discussion. This problematical species is known from a single specimen which had suffered some *post-mortem* distortion before preservation. Its status is, therefore, all the more difficult to decide.

Superficially, *H. melanopterus* is most distinctive. The lower jaw (which closes entirely within the upper) is short, narrow and pointed anteriorly. The preorbital is very shallow so that the greater part of the maxilla is exposed when the mouth is shut. This latter character, together with the peculiar arrangement of the lower jaw in relation to the upper, may be an artefact of preservation and *post-mortem* distortion. The shallow preorbital and the short, pointed lower jaw cannot, however, be attributed to these causes.

The dentition closely resembles that of *H. maxillaris* both in the form of the teeth and their restricted distribution on the premaxilla (see p. 190). The immediate question raised is, are not perhaps the shallow preorbital and the lower jaw size and shape the result of some ontogenetic disturbance in the development of an individual *H. maxillaris* ? The apparent distortion of the upper jaw might then be considered teratological rather than the result of *post-mortem* distortion.

In general appearance, *H. melanopterus* is unlike *H. maxillaris* but as Trewavas noted in her original description of the species, it is nearer the *H. maxillaris-obesus* complex than any other species group. Thus, it is impossible to give an adequate answer to the question posed above. I have decided to treat *H. melanopterus* as a distinct species mainly on the grounds that it is difficult to determine whether or not the peculiar jaws are a teratological feature, and because the nuchal and pectoral squamation of the type is manifestly smaller than in either *H. obesus* or *H. maxillaris*. Also, the rounded caudal fin is a most unusual feature in a Lake Victoria *Haplochromis*.

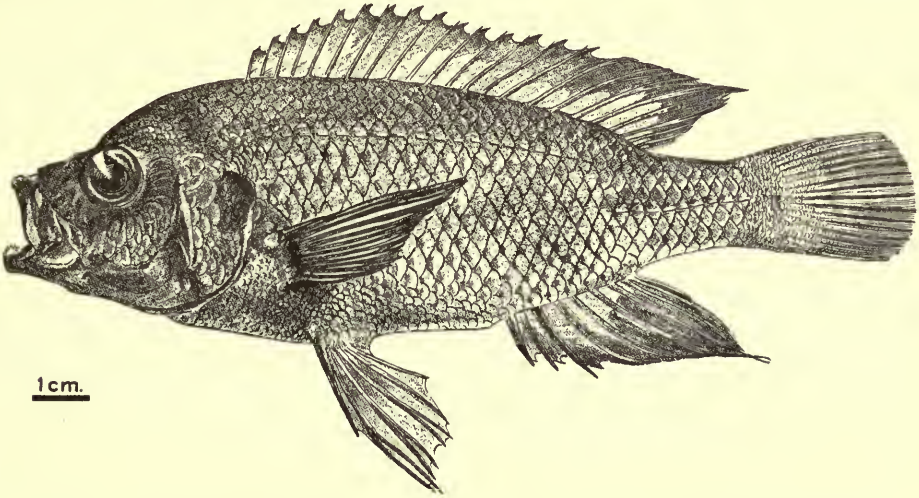

FIG. 7. *Haplochromis melanopterus* ; holotype. Drawn by Miss M. Fasken.

Description, based on the holotype, an adult male 127 mm. S.L.

Depth*	Head*	Po. %	Io. %	Snt. %	Eye %	Cheek %	L.j. %	C.P.*
35·5	33·5	11·8	27·0	30·6	28·2	23·5	37·6	14·2

* Percentage standard length.
% Percentage head-length.

Dorsal head profile very concave. Mouth probably oblique ; maxilla stout and bullate posteriorly, about three-quarters exposed even when the mouth is shut. In this specimen the mouth is open and the mandible lies horizontally, but the lateral limbs of the premaxilla and the maxillae are almost vertical. Lower jaw narrowing rapidly at a point almost half-way along its length ; greatest width contained 1·3 times in the length ; the entire lower jaw closing within the upper ; lips thickened.

Dentition very similar to that of *H. maxillaris*. Outer teeth conical, those of the upper jaw recurved and restricted to the anterior and antero-lateral aspects of the premaxilla. Teeth in the lower jaw have the crown directed anteriorly or laterally; the anterior teeth of this series are somewhat stouter than the equivalent teeth in *H. maxillaris*. Teeth of the inner series small and unicuspid, arranged in two irregular rows in each jaw.

The oral mucosa appears to have shrunk; consequently the outer teeth are more exposed than those of *H. obesus* or *H. maxillaris*, but the inner teeth are deeply embedded.

Lower pharyngeal bone broken, but apparently similar to that of *H. maxillaris*; pharyngeal teeth slender.

Gill rakers moderately coarse; ten on the lower part of the first gill-arch.

Scales ctenoid; 33 scales in the lateral line; cheek with 3 or 4 series. Nuchal and pectoral scales small. Seven scales between the dorsal fin origin and the lateral line; 9 between the pectoral and pelvic fin bases.

Fins. Dorsal with XV, 8 rays, anal with III, 8. Pectoral very slightly shorter than the head; pelvic fins with the first and second soft rays of about equal length, not quite reaching the anal fin. Caudal rounded.

Vertebrae: 14 + 16 (from a radiograph, B.M. (N.H.) Reg. No. 955A).

Colour: Adult male. Brownish dorsally, brownish-silver on the flanks and belly. Dorsal, caudal and anal fins dusky, pelvics black.

Ecology: Habitat. Smith Sound, Tanganyika Territory (2° 33′ S., 32° 50′ E.) in 12 feet of water over a mud bottom (Graham, 1929).

Food. The stomach is packed with early embryos of a cichlid fish.

Affinities. Trewavas (1929) compared *H. melanopterus* with *H. obesus* (then known only from the holotype). Now that more material of *H. obesus* is available, the resemblance is found to be less marked. In some respects the morphology of the types is similar, but in the detailed structure of the head and dentition, *H. melanopterus* would seem to be more closely allied with *H. maxillaris*. It may yet prove to be merely a teratological specimen of that species.

Haplochromis parvidens (Boulenger) 1911

(Text-fig. 8)

Paratilapia parvidens Boulenger, 1911, *Ann. Mus. Genova* (3), **5**, 65, pl. I, fig. 1; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 322 fig. 215.

Haplochromis nigrescens (Pellegrin) (part, holotype of *P. parvidens* only), Regan 1922, *Proc. zool. Soc. London*, 172.

Regan (1922) considered *H. parvidens* to be a synonym of *H. nigrescens* (Pellegrin) 1909. I have re-examined the holotypes of both species and find that, although at first sight the species do resemble one another, the dentition and form of the lower jaw in *H. parvidens* is most distinctive. Additional material now available confirms and emphasizes these differences. The two species also differ in their feeding habits; *H. nigrescens* is an insectivore and predator on small fishes, whilst *H. parvidens* is a specialized predator on embryo and larval fishes.

Haplochromis parvidens differs from the other larval and embryo fish-eating species in having a more slender and acutely pointed head, characters which typify the less specialized piscivorous predatory *Haplochromis* in Lake Victoria. The shape of the lower jaw is, however, unlike that of any predatory *Haplochromis* species (see Text-fig. 5B).

Description, based on 32 fishes (including the holotype) 63–163 mm. S.L.

Depth of body 33·3–38·2 per cent of standard length, length of head 33·3–37·5 per cent. Physiognomy relatively constant, the dorsal head profile straight or gently concave, sloping at an angle of 30°–35°. Preorbital depth 15·9–20·5 (M = 18·6) per cent of head length; least interorbital width 22·2–28·0 (M = 25·1) per cent. Snout length 1·2–1·33 times its breadth and 32·0–41·3 (M = 37·7) per cent of the head; eye diameter 20·3–27·2 (M = 23·0), depth of cheek 19·7–27·0 (M = 24·0) per cent.

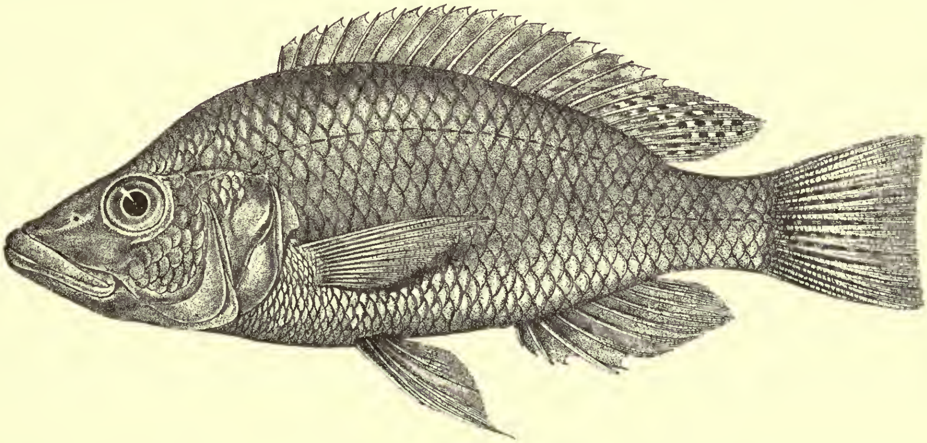

FIG. 8. *Haplochromis parvidens*; holotype (from Boulenger, *Ann. Mus. Genova*, 1911).

Caudal peduncle 13·6–16·8 per cent of standard length, 1·1–1·5 times as long as deep (modal range 1·3–1·4 times).

Mouth widely distensible and protractile, slightly oblique or horizontal when closed. Lips thickened. Lower jaw of a characteristic shape (Text-fig. 5B), somewhat rounded in cross-section and narrowing rapidly from a point about half-way along its length; consequently, the anterior part closes within the upper jaw. Length of lower jaw 43·3–55·5 (M = 48·0) per cent of head length (showing a weak positive allometry with standard length) and 1·5–2·5 (modal range 1·9–2·1) times its width. Posterior tip of the maxilla bullate and almost completely hidden beneath the preorbital, usually not reaching the vertical to the anterior orbital margin, but extending to below the anterior part of the eye in a few specimens.

Gill rakers. Nine to 11 (rarely 8 or 12, mode 10) on the lower part of the first gill-arch.

Scales ctenoid; lateral line with 30 (f.2), 31 (f.14), 32 (f.15) or 33 (f.1) scales. Cheek with 3 or 4 series; 6 or 7 (rarely 5) scales between the origin of the dorsal fin and the lateral line; 6 or 7 (less frequently 5) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.1), 24 (f.10), 25 (f.19) or 26 (f.2) rays, anal with 11 (f.9), 12 (f.22) or 13 (f.1), comprising XV–XVI (rarely XIV), 9 or 10 (rarely 8) and III, 8 or 9 (rarely 10) spinous and branched rays for the fins respectively. Pectoral fin shorter than the head. First soft ray of the pelvic fin produced and extending to the anal fin; proportionately longer in adult males.

Teeth. Both the inner and outer rows of teeth are deeply embedded in the oral epithelium, with the inner series often completely hidden. The outer teeth are mainly biscuspid in fishes 63–110 mm. S.L., with some unicuspids present in larger individuals. In fishes above this size, the outer teeth are predominantly unicuspid, relatively slender and recurved; laterally placed teeth point inwards. In the three skeletons available, there are 50, 54 and 62 outer teeth in the upper jaw.

Teeth in the inner series are small, slender and weakly tricuspid in fishes less than 115 mm. S.L., but are unicuspid in larger individuals. In most fishes, the inner teeth are implanted almost horizontally, so that their crowns point backwards. One or two (rarely three) series of inner teeth occur in each jaw and are separated from the outer teeth by a small but distinct interspace.

Lower pharyngeal bone with a triangular dentigerous surface, 1·1–1·2 times as broad as long or, rarely, somewhat wider. Lower pharyngeal teeth fine and cuspidate.

Syncranium. The premaxilla and the dentary of *H. parvidens* are outstanding osteological characters. In combination they are diagnostic of the species.

In *H. parvidens*, the premaxillary pedicels are as long as, or longer than the dentigerous limb of the bone, whereas in the majority of Lake Victoria *Haplochromis* (including the large-mouthed species) the pedicels are shorter.

The mandible has been described above; its skeleton clearly shows the marked anterior narrowing and the peculiar lateral bullation of the area surrounding the bifurcation into ascending and horizontal rami (a similar swelling is also seen in *H. obesus* and *H. maxillaris*).

The maxilla is strictly comparable with that of *H. obesus* and *H. maxillaris*, but the neurocranium differs in having an elongate preorbital face. The preorbital part of the skull is about one-third of the basilar length as compared with one-fifth to one-quarter in generalized *Haplochromis*. In this respect the neurocranium of *H. parvidens* resembles that of a small predatory *Haplochromis* such as *H. nigrescens*.

Vertebrae: 13 + 16 in two skeletons examined.

Coloration in life: Adult males. Ground colour dark blue-black dorsally, silvery-blue ventrally. Dorsal fin sooty, with orange-red lappets; caudal sooty, the dorsal and ventral tips orange-red. Anal fin deep maroon, with two or three red ocelli. Pelvics black. Coloration of *immature males* unknown. *Females.* Ground colour an overall olivaceous-green, with faint indications of five to nine dark transverse bars. All fins olivaceous.

Colour in preserved material: Adult and immature males. Dark brown, some adults almost black; faint traces of five to nine transverse bars may be visible on the flanks and caudal peduncle. Dorsal fin dark, the soft part faintly maculate; pelvics black; anal and caudal fins dusky. *Females.* Golden-brown ground coloration, some faintly barred. All fins hyaline, the dorsal and caudal fins sometimes maculate.

Distribution. Lake Victoria and Lake Salisbury (a single specimen in the collections of the Uganda Game and Fisheries Department, Entebbe).

Ecology: Habitat. Like *H. maxillaris* and *H. obesus, Haplochromis parvidens* is apparently confined to littoral and sublittoral zones where the water is less than 50 feet deep. Unlike the former species, however, *H. parvidens* is less closely restricted to a particular substrate. Although all three species have been caught in the same habitat, the available data suggest that *H. parvidens* may be the only member of this trophic group to occur commonly over a mud bottom.

Food. Seventeen of the 60 specimens examined had food in the stomach; of these, 15 had eaten cichlid embryos or larvae. The stomachs of the two other fishes were filled with a fatty, yellow, yolk-like substance.

Breeding. There is no information on the breeding habits of *H. parvidens.* Fishes less than 105 mm. S.L. are immature; there is no apparent correlation between sex and maximum adult size.

Affinities. Despite the deeply embedded teeth, long premaxillary pedicels and unusual lower jaw, there is an overall similarity between *H. parvidens* and some of the structurally less-specialized predatory *Haplochromis. Haplochromis nigrescens,* with which *H. parvidens* was previously synonymized, exemplifies this apparent relationship. There is also some similarity between *H. parvidens* and *H. cryptodon,* and more particularly with *H. microdon. Haplochromis parvidens* could have evolved from either an *H. nigrescens*-like stem or from a species resembling *H. cryptodon.*

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
Genoa Museum (Holotype)	Ripon Falls, Jinja	Bayon.
B.M. (N.H.)—1911.3.3.33	,, ,,	,,
,, 1958.1.16.95	Kaianje	E.A.F.R.O.
,, 1958.1.16.96–98	Entebbe Harbour	,,
,, 1958.1.99	Busungwe Bay	,,
,, 1958.1.16.100	Ekunu Bay	,,
,, 1958.1.16.101	Napoleon Gulf, near Jinja	,,
,, 1958.1.16.108	,, ,,	,,
,, 1958.1.16.130–139	,, ,,	,,
,, 1958.1.16.107	Macdonald Bay	,,
,, 1958.1.16.109–113	Pilkington Bay	,,
,, 1958.1.16.114–115	Njoga, Williams Bay	,,
,, 1958.1.16.116–129	Beach near Nasu Point, Buvuma Channel	,,
	Kenya	
,, 1958.1.16.104–106	Kisumu Harbour	,,
	Tanganyika	
,, 1958.1.16.92–94	Mwanza, Capri Bay	,,

Museum and Reg. No.	Locality	Collector
	Lake Victoria, Locality Unknown	
„ 1958.1.16.102–103 .	— .	„
„ 1928.5.24.112 .	— .	M. Graham.
„ 1928.5.24.399–400 .	— .	„
„ 1928.5.24.401–402 .	— .	„

Haplochromis cryptodon sp. nov.

Holotype. A male, 123 mm. standard length, from a beach near Nasu Point, Buvuma Channel, Uganda.

Description, based on 31 specimens (including the holotype) 92–130 mm. standard length.

Depth of body 27·5–35·6 per cent of standard length, length of head 30·3–34·9 per cent. Physiognomy relatively uniform, the dorsal head profile straight and sloping at an angle of 35°–40°.

Preorbital depth 12·5–17·6 (M = 15·4) per cent of head length, least interorbital width 21·2–25·7 (M = 23·6) per cent. Snout as broad as long or very slightly broader, its length 27·5–34·2 (M = 31·3) per cent of head ; eye 23·1–29·4 (M = 25·8), depth of cheek 17·7–25·7 (M = 23·6) per cent.

Caudal peduncle 14·7–17·7 per cent of standard length, 1·3–1·7 (modal range 1·3–1·5) times as long as deep.

(Four specimens [two from near Nasu Point, Buvuma Channel, Uganda, and two from Majita, Tanganyika Territory] differ in being noticeably more slender [depth 27·5–31·0 per cent S.L.] and in having less steeply sloping heads. The two Uganda specimens also have a somewhat longer lower jaw [46·0 per cent head length] than is modal. In all other characters these specimens agree with the generality of individuals. Since they are amongst the five smallest specimens available, it is possible that their divergent characters may be " juvenile ").

Mouth slightly oblique and moderately distensible ; lips slightly thickened. Posterior tip of the maxilla somewhat bullate and reaching or almost reaching the vertical to the anterior orbital margin. Lower jaw with a tendency to narrow rather abruptly at about its mid-point, but not narrowing so markedly as in *H. parvidens* ; in some specimens (particularly individuals less than 100 mm. S.L.) this character is only visible after dissection. Length of lower jaw 39·2–46·5 (M = 42·3) per cent of head length, 1·3–1·9 (modal range 1·5–1·6) times as long as broad.

Gill rakers moderately slender, 10 or 11 (less frequently 9), on the lower limb of the anterior arch.

Scales ctenoid ; lateral line with 30 (f.2), 31 (f.7), 32 (f.17), 33 (f.2) or 34 (f.2) scales. Cheek with 2 or 3 (rarely 4) series ; 5–7 scales between the lateral line and the origin of the dorsal fin ; 6–8 (rarely 9) between the pectoral and pelvic fin insertions.

Fins. Dorsal with 23 (f.1), 24 (f.14) or 25 (f.16) rays, anal with 11 (f.7), 12 (f.23) or 13 (f.1) comprising XV–XVI, 9 or 10 (rarely 8) and III, 8 or 9 (rarely 10) spinous and soft rays for the fins respectively. Pectoral fins shorter than the head. First pelvic ray produced and extending to the spinous part of the anal.

Teeth. The inner and outer series of teeth are deeply embedded in the oral epithelium, so that only the tips of the outer teeth are visible. In specimens less than 100 mm. S.L. the outer teeth are weakly and unequally bicuspid. In larger fishes this row is composed of small, unicuspid and slightly recurved teeth.

Teeth in the inner series are either unicuspid or weakly tricuspid, and are arranged in one or two rows. In fresh material it is usually impossible to see these teeth unless the oral mucosa is dissected away.

Lower pharyngeal bone triangular, its dentigerous area 1·0–1·5 times as broad as long ; pharyngeal teeth slender and cuspidate.

Syncranium. The syncranium of *H. cryptodon* resembles the generalized *Haplochromis* type, except that the maxilla is somewhat stouter and the dentary shows an incipient departure from the generalized condition towards that of *H. parvidens* (see p. 196 and text fig. 5B).

Vertebrae : 14 + 16 in the single specimen examined (Radiograph, B.M. (N.H.) Reg. No. 958).

Coloration in life : Adult and immature females. Ground colour dark green-brown shading to light gold ventrally. All fins hyaline. The live coloration of *males* is unknown.

Colour of preserved material : Adult males. Ground colour dark gun-metal dorsally, shading to greyish-green on the flanks and ventral surfaces ; chest and branchiostegal membrane dusky ; faint traces of a coppery sheen on the operculum and flanks. Five to seven faint but dark transverse bars are visible on the flanks and caudal peduncle. Dorsal fin dusky ; caudal and anal fins hyaline, the latter with two to four dead-white ocelli ; pelvic fins black. *Females.* Ground colour light golden-yellow, slightly darker dorsally ; in some individuals there are faint traces of about five, broad, transverse bands on the flanks. One adult is of particular interest since it displays incipient male coloration ; the pelvic fins are dusky as are the chest and branchiostegal membrane. In addition there are traces of a coppery sheen on the operculum.

Distribution. Habitat. H. cryptodon has been recorded from only three localities, namely, the Napoleon Gulf near Jinja, a beach near Nasu Point (Buvuma Channel) and a beach at Majita, Tanganyika Territory. The apparent absence of *H. crytodon* from other localities is difficult to explain since it was one of the more abundant species at the Nasu Point station and formed a regular element of the seine-net catches there. Perhaps it is significant that the majority of *H. cryptodon* caught at Nasu Point were brooding or " ripe " females, thus suggesting that the area is used as a breeding ground. If this is so, the species may normally occur in some other habitat which could not be fished by conventional gear.

Food. Only one fish, a female from Nasu Point, had ingested material in the stomach and intestine. The stomach was packed with recently fertilized cichlid ova, whilst numerous small fish vertebrae were found in the posterior intestine. The stomach contents may have been the female's own brood, but the presence of larval fish vertebrae in the faeces cannot be explained on the same grounds.

With such little positive evidence it is impossible to generalize on the feeding habits of *H. cryptodon.* But the single record of gut-contents, taken together with the jaw structure of this species, suggests a diet of embryo and larval fishes.

Breeding. *H. cryptodon* is a female mouth-brooder. The smallest individual caught, a female 92 mm. S.L., was sexually mature. Males and females reach the same adult size.

Affinities. With the exception of *H. cronus*, *H. cryptodon* is the most generalized of the species referred to this trophic group. In structure and proportions it shows greater affinity with *H. microdon* and *H. parvidens* than with the *H. obesus-H. maxillaris-H. cronus* section of the group. *H. cryptodon* was probably evolved from the complex of piscivorous-insectivorous species which are not markedly differentiated (except for their larger size) from the generalized *Haplochromis* stock in Lake Victoria.

Diagnosis. From the generality of Lake Victoria *Haplochromis* species, *H. cryptodon* may be distinguished by its distensible mouth and almost completely hidden dentition. From other species showing these characters, it is distinguished by the shape of the head (and particularly of the lower jaw) and an absence of teeth with anteriorly directed crowns.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1958.1.16.31 (Holotype, *H. cryptodon*) .	Beach near Nasu Point, Buvuma Channel .	E.A.F.R.O.
,, 1958.1.26.32–33 .	,, .	,,
,, 1958.1.16.37–62 .	,, .	,,
,, 1958.1.16.34 .	Napoleon Gulf, near Jinja .	,,
	Tanganyika	
,, 1958.1.16.35–36 .	Majita .	,,

Haplochromis microdon (Boulenger) 1906

(Text-fig. 9)

Pelmatochromis microdon (part; holotype only) Blgr., 1906, *Ann. Mag. nat. Hist.* (7) **17**, 441; *Idem*, 1913, *Cat. Afr. Fish.* **3**, 412, fig. 282.

Haplochromis microdon (Blgr.), (part), Regan, 1922, *Proc. Zool. Soc., London*, 173.

When redefining *H. microdon* Regan (1922) noted his belief that the type specimen had a malformed lower jaw (which did not bite against the upper) and that its small teeth were due to this malformation. In the light of additional specimens, I am unable to agree with Regan, and conclude that the shape of the lower jaw and its small teeth are, indeed, some of the diagnostic characters of the species. Consequently, I find that the other species which Regan referred to *H. microdon* can no longer be considered conspecific; they will be dealt with in a subsequent paper.

The peculiar lower jaw of *H. microdon* closely resembles that of *H. parvidens* but the two species differ in other osteological characters.

Description, based on eight specimens (including the holotype) 114–148 mm. S.L.

Depth of body 33·1–37·6 per cent standard length, length of head 31·2–34·8 per cent. Physiognomy variable and dependent on whether the dorsal head profile is moderately or strongly concave. Preorbital depth 14·6–18·8 (M = 17·1) per cent of head length, least interorbital width 24·6–29·6 (M = 26·6) per cent. Snout as long as broad or very slightly longer; its length 30·8–34·5 (M = 32·5) per cent of head, eye diameter 24·0–28·2 (M = 25·5), depth of cheek 19·2–26·0 (M = 23·8) per cent.

Caudal peduncle 15·3–17·0 per cent of standard length, 1·3–1·5 times as long as deep.

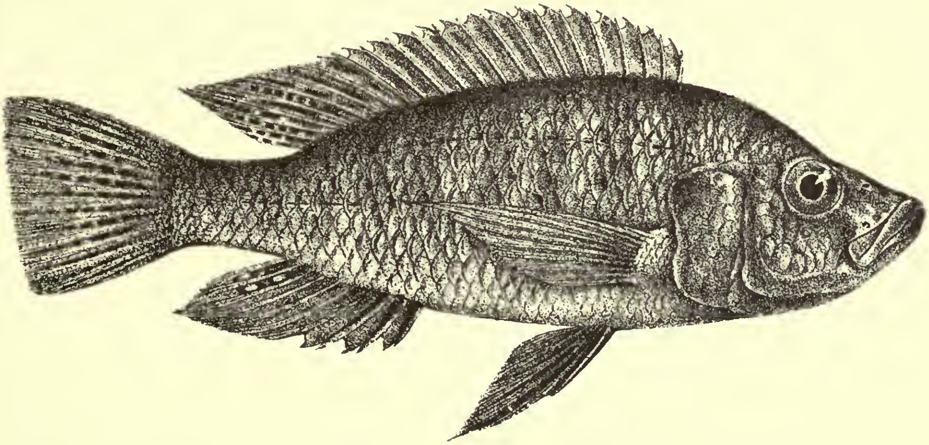

FIG. 9. *Haplochromis microdon*; holotype (from Boulenger, *Fishes of the Nile*).

Mouth oblique, distensible and moderately protractile. Jaws equal anteriorly or the lower very slightly shorter; lower jaw always closing within the upper, its length 43·5–48·0 (M = 46·2) per cent of head length, 1·6–2·3 (modal range 1·9–2·2) times as long as broad. Premaxillary pedicels shorter than the dentigerous limb. Posterior tip of the maxilla slightly bullate, partly hidden by the preorbital and extending to the vertical to the anterior orbital margin, or almost so.

[One specimen, an adult female 114·0 mm. S.L., from Pilkington Bay, is not included in the general description given above. Although it differs sufficiently from the other specimens to raise doubts as to its identity, I do not consider it to be a distinct species. The possibility of this fish being a hybrid between *H. microdon* and some other species (? *H. parvidens*) cannot, however, be excluded.

The dentition and lower jaw are of the "*microdon-parvidens*" type, but the dentary is narrower anteriorly and it is shorter than even the extreme specimens of either species. These characters, coupled with the large eye and short snout give this fish an unusual appearance which departs from both the "*microdon*" and the "*parvidens*" types. The mouth is oblique and the premaxillary pedicels short, so that the sum of characters places the specimen nearest *H. microdon*.

The principal morphometric characters are :

Depth*	Head*	Po. %	Io. %	Snt. %	Eye %	Cheek %	L.j. %	C.P.*
33·3	34·2	18·0	25·2	29·5	30·8	20·5	41·0	15·8

* Percentage S.L.
% Percentage head-length.]

Gill-rakers slender, 9–11 (mode 11) on the lower part of the anterior arch.

Scales ctenoid ; lateral line with 30 (f.2), 32 (f.4) or 33 (f.2) scales.

Fins. Dorsal fin with 24 (f.4) or 25 (f.4) rays, anal with 10 (f.1), 11 (f.3) or 12 (f.4), comprising XV–XVI, 9 or 10 and III, 7–9 spinous and branched rays for the fins respectively. Pectoral fin shorter than the head ; first soft pelvic ray produced, reaching to the vent in females and to the spinous anal fin in males.

Teeth. All the teeth are so deeply embedded in the oral epithelium that they are invisible in fresh material. The teeth in the outer series of both jaws are small, unicuspid and slightly recurved. The single or rarely double row of unicuspid inner teeth is implanted at an acute angle. A distinct interspace separates the inner and outer series of teeth.

Lower pharyngeal bone triangular, the dentigerous area slightly broader than long ; lower pharyngeal teeth slender and cuspidate.

Syncranium (from a radiograph, B.M. (N.H.) Reg. No. 961, and a partial dissection). The dentary is almost identical with that of *H. parvidens*, but is more slender. The premaxilla is of a generalized type and does not have the elongated pedicels which characterize *H. parvidens*. The neurocranium is apparently intermediate between that of *H. cryptodon* and that of *H. parvidens*.

Colour of preserved specimens : Adult males. Ground colour very dark brown, the ventral abdominal region lighter in one specimen ; five or six, broad and dark transverse bars visible on the flanks of some individuals. Branchiostegal membrane black. Dorsal, caudal, pelvic and anal fins dark, almost black, the anal with four, whitish ocelli.

Adult females. Ground colour greyish-brown, darker dorsally ; very faint indications of five or six broad transverse bars on the flanks. Dorsal, anal, and caudal fins hyaline, the last weakly maculate especially on the upper half ; pelvic fins black.

Distribution. Lake Victoria.

Ecology : Habitat. Seven of the eight fishes examined were from littoral zones of the lake, and were taken over both firm and soft substrates ; two were caught at a depth of 30–36 feet and the others in water 6–12 feet deep. The habitat of the eighth specimen is not known.

Food unknown. Since the dentition and jaw structure of *H. microdon* so closely resemble those of *H. parvidens*, the feeding habits of the two species may well be similar.

Breeding. No data are available ; the eight specimens are all adults.

Affinities. The most obvious relative of *H. microdon* is *H. parvidens* ; the lower jaw in both species is of a type otherwise unrepresented in the Lake Victoria *Haplochromis* species flock. The dentary of *H. microdon* is, however, a more extreme modification of the generalized type than is the dentary of *H. parvidens*. On the other hand the elongated premaxillary pedicels of *H. parvidens* do not occur in *H. microdon* which retains a premaxilla of the generalized type. Consequently the mouth is less protrusible in this species. *H. parvidens*, in its gross morphology, and particularly in the shape of its neurocranium, shows strong affinity with some of the piscivorous predators (e.g. *H. nigrescens*). In corresponding characters, *H. microdon* is near *H. cryptodon*, from which it could be derived by further specialization of the lower jaw. Thus, the resemblance between *H. microdon* and *H. parvidens* may be the result of convergent evolutionary trends.

Diagnosis. *Haplochromis microdon* may be distinguished from other species with deeply embedded teeth by the shape of the lower jaw, the concave dorsal head profile and the oblique mouth. It may be further distinguished from *H. parvidens* by its having premaxillary pedicels which are shorter than the horizontal (dentigerous) limb of this bone.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.309 (Holotype *Pelmatochromis microdon*)	Bunjako	Degen.
,, 1958.1.16.24	Pilkington Bay	E.A.F.R.O.
,, 1958.1.16.25	Entebbe Harbour	,,
,, 1958.1.16.26	Ekunu Bay	,,
,, 1958.1.16.29–30	Beach near Nasu Point, Buvuma Channel	,,
	Lake Victoria, Locality Unknown	
,, 1958.1.16.27–28	—	,,

DISCUSSION

The embryo-larval fish-eating habits of this species-group were briefly mentioned in the introduction. As far as I can determine from published accounts, no other African cichlids have occupied this particular niché.

That the group preys almost exclusively on the embryos and larvae of other cichlids is probably due to the fact that only the Cichlidae breed continuously; the non-cichlid fishes spawn biannually, at the periods of maximum rainfall. On the other hand, the mouth-brooding habits of most Lake Victoria *Haplochromis*, and both *Tilapia* species, would seem to provide very little opportunity for these predators unless they have evolved a method of forcing the parent to jettison its brood. Since embryos at all stages of development have been found in the stomach contents, it is clear that the species do not obtain their food solely by preying on newly fertilized eggs before these are picked up by the brooding parent. The method of attack is unknown, but from the large number of embryos or larvae taken it must be highly efficient.

Two anatomical features (a distensible and somewhat protrusible mouth, and a weak to moderately developed dentition deeply embedded in the thickened oral epithelium) characterize six of the seven species in this trophic group. It is not known if either of the characters has any functional significance in connection with the feeding habits. The seventh species, *H. cronus*, has strong and fully-exposed teeth, and the mouth is not noticeably distensible or protractile. Unfortunately, only a few specimens of *H. cronus* had food in the stomach. However, it may be significant that these fishes had fed on larger (*ca.* 11 mm.) late larvae, whilst members of the other species had fed on embryos and early larvae. That is to say, *H. cronus* had taken young of an age when they frequently leave the parent's mouth for short periods. Those species with distensible, protractile mouths and hidden teeth had taken mainly intra-oral young. Perhaps these larger mouthed species engulf the head or mouth of a brooding female and in this way force the parent to abandon its young?

As in most other trophically defined species-groups there is evidence of both phyletic and convergent relationships between the species. But, unlike most others, this group shows greater divergence and more tenuous relationships within the apparently phyletic lines.

Haplochromis cronus is the least specialized species, but it differs from the generality of Lake Victoria *Haplochromis* in having the caudal fin almost completely scaled (a characteristic of Lake Nyasa *Haplochromis*).

Haplochromis obesus and *H. maxillaris* seem to be much specialized derivatives of a form resembling *H. cronus*, but neither of these species has a scaled caudal fin. The dentition is similar in *H. obesus* and *H. maxillaris* and quite unlike that of *H. cronus* ; in other characters (especially the shape of the lower jaw) the two species are markedly different. It is, in fact, impossible to decide whether the species are of the same lineage or the descendants of distinct but related ancestral stocks.

A similar state of affairs exists when *H. cryptodon* and *H. microdon* are considered. A further complication is introduced by the resemblance between *H. microdon* and *H. parvidens*. In this case, however, it is possible that *H. microdon* was derived from an *H. cryptodon*-like ancestor, and *H. parvidens* from one of the less-specialized piscivorous predators.

In all these species, anatomical differences between members of possible lineages are certainly greater than those encountered between species in the algal-grazing and mollusc-" shelling " groups (Greenwood, 1956*b* and 1957).

Two of the species described above, *H. obesus* and *H. maxillaris*, clearly demonstrate a phenomenon which is common amongst the Lake Victoria *Haplochromis*, namely, the intraspecific constancy of certain osteological and dental characters contrasting with the variability of other and often anatomically related characters. For example, the lower jaw and dentition of *H. obesus* is readily diagnostic, whilst the physiognomy is so variable that difficulty would be experienced in identifying some specimens were it not for the characteristic lower jaw. Likewise, there is marked variation in the gross morphology of *H. maxillaris*, yet the dentary and the dentition of both jaws are relatively constant. *Haplochromis parvidens*, however, shows only slight variation in its gross morphology.

In certain characters, *Haplochromis taurinus* Trewavas, of Lake Edward, resembles fishes of the *H. maxillaris-H. obesus* complex. The shape of the head approaches that of *H. maxillaris*, particularly with regard to the stout jaws and thickened lips; also, the outer teeth in the upper jaw are hidden by a fold of lip-tissue. The likeness does not extend to the dentition, which is a critical character in this group. The teeth of *H. taurinus* are large, distinct and biscuspid (at least in the holotype, a fish 164 mm. total length) and are of a form rarely encountered in any Lake Victoria *Haplochromis*. There can be little doubt therefore, that the resemblance between *H. taurinus* and *H. maxillaris* or *H. obesus* is superficial and of little phyletic significance.

Haplochromis plagiodon Regan & Trewavas 1928

(Text-fig. 10)

Haplochromis crassilabris Blgr. (part), 1906, *Ann. Mag. nat. Hist.* (7) **17**, 445.
Paratilapia crassilabris (Blgr.), part, Blgr., 1915, *Cat. Afr. Fish.* **3**, 345.
Haplochromis crassilabris Blgr. (part), Regan, 1922, *Proc. zool. Soc. London*, 167.
Hemitilapia bayoni Blgr. (part), Blgr., 1908, *Ann. Mus. Genova* (3), **4**, 6; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 491.
Clinodon bayoni (Blgr.) (part), Regan, 1920, *Ann. Mag. nat. Hist.* (9) **5**, 45 (footnote).
Haplochromis obliquidens Hilgendorf (part), Regan, 1922, *Proc. zool. Soc. London*, 188.
Haplochromis plagiodon Regan & Trewavas, 1928, *Ann. Mag. nat. Hist.* (10), **2**, 224.

Description, based on five specimens (including the holotype), 56–85 mm. standard length.

H. plagiodon is a generalized species, except that it has teeth of an unusual form, resembling stout and somewhat modified versions of the teeth found in *H. lividus* Greenwood. Although *H. plagiodon* is represented by only five specimens, the form of the teeth is sufficiently distinctive and constant to warrant the assumption that the species is biologically valid.

The principal morphometric characters for each of the five specimens are tabulated. below. All are males.

S.L.	Depth*	Head*	Po. %	Io. %	Snt. %	Eye %	Cheek %	L.j. %	C.P.*
56·0	35·7	31·2	13·1	25·7	28·6	30·2	21·7	34·2	17·0
72·0	36·0	30·5	15·0	27·2	27·2	29·2	22·7	36·3	16·7
76·0	36·8	31·6	15·9	25·0	29·2	31·3	23·0	37·5	15·2
†81·0	32·7	29·6	16·7	28·4	29·2	28·4	20·8	34·6	18·0
85·0	36·5	30·3	15·6	26·9	26·9	30·8	23·0	34·6	16·5

* Percentage standard length.
% Percentage head length.
† Holotype.

Dorsal head profile straight and steeply sloping (*ca.* 50°). Mouth horizontal; posterior tip of the maxilla extending to the vertical to the anterior orbital margin, or slightly beyond. Jaws equal anteriorly, the lower 1·3–1·6 times as long as broad; lips not thickened.

Teeth. Outer teeth stout, erect and bicuspid, with the major cusp obliquely truncate and somewhat compressed, the minor cusp conical. In one specimen

(72 mm. S.L.) the teeth are very worn, so that the minor cusp is indicated merely as a faint groove on the labial aspect of the tooth. There are 30–38 teeth in the outer series of the upper jaw.

In most respects, the shape of these teeth closely resembles one of the variants occurring in *H. lividus* (see Text-fig. 2B in Greenwood, 1956*b*), except that in *H. plagiodon* the teeth are not recurved, are stouter and do not have a distinct neck.

The inner teeth are tricuspid and arranged in two or three rows in each jaw and are separated from the outer row by a distinct interspace.

Lower pharyngeal bone triangular, fairly stout (as compared with, for example, fishes of the *H. lividus-H. nuchisquamulatus* group); dentigerous area 1·2–1·5 times as broad as long. Lower pharyngeal teeth cuspidate, those of the two median series enlarged; conical in three specimens but cuspidate in two others.

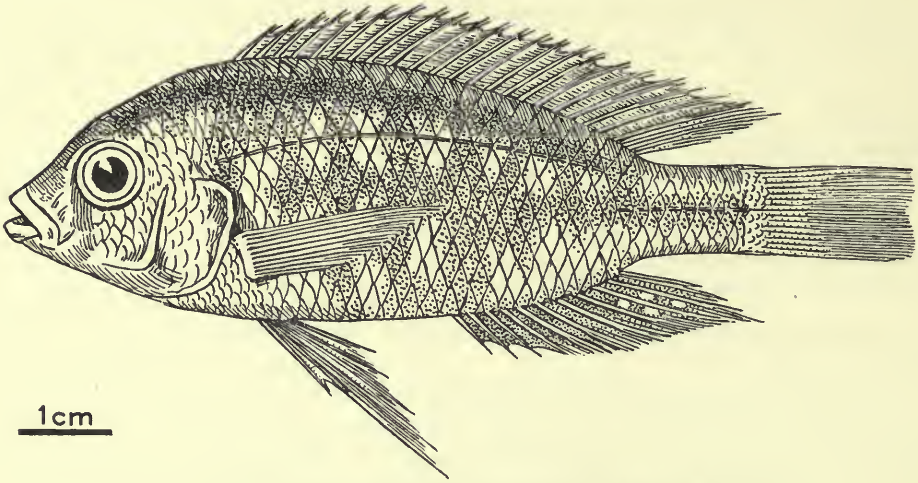

FIG. 10. *Haplochromis plagiodon*. Drawn by Miss D. Fitchew.

Gill rakers short and stout; 7 or 8 on the lower limb of the anterior arch.

Scales ctenoid; lateral line with 31 (f.1), 32 (f.3) or 33 (f.1) scales. Cheek with 3 or 4 (rarely 2) series; 6 or 7 scales between the dorsal fin origin and the lateral line, 8 or 9 between the pelvic and pectoral fin bases.

Fins. Dorsal with 24 (f.1), 25 (f.2) or 26 (f.2) rays, anal with 11 (f.1), 12 (f.3) or 13 (f.1) comprising XV–XVI, 9 or 10 and III, 8–10 spinous and branched rays for the fins respectively. First soft pelvic ray produced and extending to the spinous part of the anal fin. Pectoral fin slightly shorter than the head.

Coloration. Unknown in life and known only for preserved males. Ground colour silver-grey to brownish-grey; eight to ten transverse bars on the flanks and caudal peduncle, a fairly well-defined mid-lateral stripe, with indications of an interrupted band running slightly above the upper lateral line. Faint traces of two interocular bands and a lachrymal stripe. Dorsal, caudal and anal fins pale and immaculate;

six to eight small ocelli arranged in two rows on the anal fin. Pelvic fins dusky on the outer two-thirds in two specimens and entirely pale in the remainder.

Ecology. No ecological data are available for the type and one other specimen; the three other fishes were caught in a seine-net operated in shallow water over an exposed, sandy beach at Entebbe, Uganda, In two of these specimens, remains of larval Diptera and Ephemeroptera (together with many fine sand grains) were found in the intestines.

Diagnosis and affinities. Haplochromis plagiodon may be distinguished from other species in Lake Victoria by its peculiar teeth. The relatively coarse lower pharyngeal bone and the enlarged median pharyngeal teeth, together with the stout, firmly implanted and few (30–36) outer teeth, separate *H. plagiodon* from the two other species (*H. lividus* and *H. nuchisquamulatus*) with obliquely truncated, biscuspid outer teeth.

Regan & Trewavas (1928) compared the teeth of *H. plagiodon* holotype with those of the type of *Bayonia xenodonta* Blgr. (now considered a synonym of *Macropleurodus bicolor* (Blgr.), Greenwood, 1956*a*). They emphasized the differences existing between the two species, even though there appeared to be some resemblance in the shape of the teeth. Now that additional specimens of comparable sizes are available for both species, it is clearer than ever that *H. plagiodon* is not closely related to *Macropleurodus bicolor.* Regan & Trewavas also suggested that *H. plagiodon* might be related to *H. humilior* (Blgr.). Although both these species have somewhat enlarged lower pharyngeal bones and median pharyngeal teeth, the resemblance in gross morphology is less marked and ceases when the oral dentition is compared. Likewise, although the oral teeth of *H. plagiodon* resemble those of *H. lividus*, the latter species has a fine lower pharyngeal bone with slender, cuspidate median teeth, and finer, more numerous oral teeth.

Thus, it is only possible to suggest that *H. plagiodon* represents an independent offshoot from the generalized *Haplochromis* stem.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1909.5.4.29 (Holotype *H. plagiodon*)	Sesse Isles	Bayon.
,, 1906.5.30.427	Entebbe	Degen.
,, 1958.1.16.245–247	Entebbe, Bugonga Beach	E.A.F.R.O.

Haplochromis chilotes (Blgr.) 1911

(Text-fig. 11)

Paratilapia chilotes Blgr., 1911, *Ann. Mus. Genova* (3), **5**, 68, pl. II, fig. 2; *Idem, Cat. Afr. Fish.* **3**, 338, fig. 228.

Haplochromis chilotes (Blgr.), Regan, 1922, *Proc. zool. Soc. London*, 170.

As defined below, *H. chilotes* exhibits a high degree of individual variability. The species may be divided into two morphotypes : first, those individuals with hypertrophied and lobed lips and secondly, those in which the lips are thickened but not produced into well-defined lobes. Seventeen of the 25 specimens available fall into the first category and eight into the second. The division is not sharp, however, since the lips of some individuals in the second category do have a lobe-like, median swelling.

Certain other characters are apparently correlated with the extent of lip development. For example, in most specimens with strongly lobed lips, the upper dental arcade is narrow and acutely rounded anteriorly. Also, in these fishes, the lower jaw is usually longer. The correlation is not complete and some lobe-lipped fishes have a mixture of these characters. It is because the sample as a whole shows a complete intergradation of lip, jaw and dental characters that I consider the material to represent a single species. Furthermore, I can discover no ecological differences between the two morphotypes, nor is there any obvious difference in the breeding coloration of the males. Nevertheless, the present arrangement should probably be considered tentative until more material and further field observations are available.

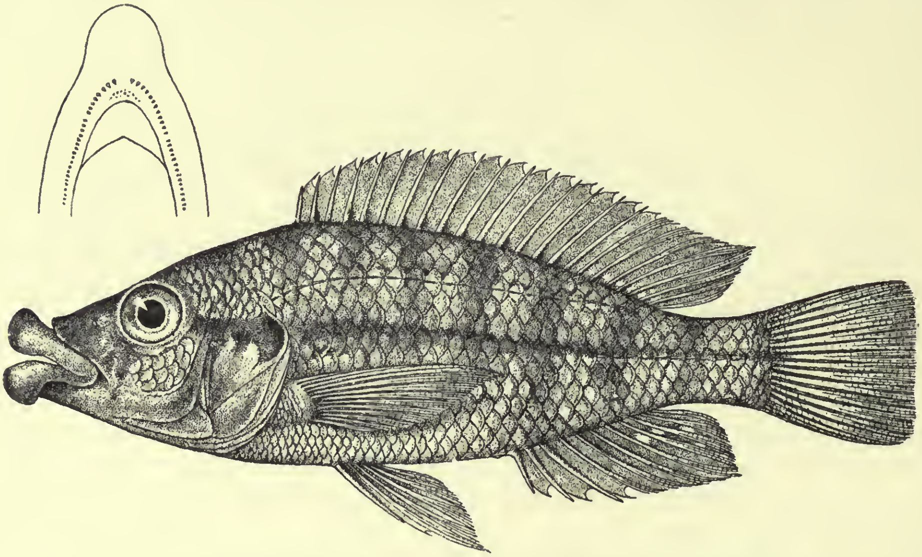

FIG. 11. *Haplochromis chilotes ;* holotype (from Boulenger, *Fishes of the Nile*).

Description, based on 25 specimens (including the holotype) 70–148 mm. standard length.

Depth of body 32·5–40·8 per cent of standard length ; length of head (excluding the lips) apparently correlated with the degree of lip hypertrophy, 31·4–34·7 (M = 32·7) per cent of standard length in fishes without clearly lobed lips and 32·0–38·2 (M = 35·5) per cent in those with lobed lips. Dorsal head profile straight and gently sloping, or slightly decurved. Preorbital depth 15·0–18·2 (M = 16·8) per cent of head ; least interorbital width 19·3–27·2 (M = 23·8) ; snout longer than broad in lobe-lipped fishes and as broad as long in others, its length 30·8–38·4 (M = 34·0) per cent of head; eye 28·6–21·8 (M = 25·4), depth of cheek 18·1–25·4 (M = 20·5) per cent.

Caudal peduncle 12·5–17·2 (M = 15·3) per cent of standard length.

Mouth horizontal, posterior tip of the maxilla reaching or almost reaching the vertical to the anterior orbital margin. Lips thickened, grossly so in some specimens in which each lip is produced medially into a tongue-shaped or globose lobe; in others there may be an incipient lobe or even no indication of any such development. Jaws equal anteriorly, the lower proportionately longer (36·0–49·0, M = 39·6 per cent of head) in fishes with lobed lips than in the others (30·0–36·6, M = 33·2 per cent).

Gill-rakers short and stout, 7–9 on the lower limb of the anterior arch.

Scales ctenoid; lateral line with 31 (f.3), 32 (f.10), 33 (f.9), 34 (f.2) or 35 (f.1) scales. Cheek with 3 (rarely 2 or 4) series. Seven or 8 (rarely 6) scales between the origin of the dorsal fin and the lateral line; 8 or 9 (less commonly 6, 7 or 10) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.3), 25 (f.18) or 26 (f.4) rays, anal with 11 (f.3) or 12 (f.22), comprising XV–XVI, 9 or 10 and III, 8 or 9 spinous and branched rays for the fins respectively. Pectoral fin shorter than the head; first soft pelvic ray produced, variable in its posterior extension but proportionately longer in adult males than females. Caudal subtruncate.

Teeth. In most specimens with hypertrophied and lobed lips the outer teeth in the upper jaw are arranged in an acutely rounded arcade, a pattern not found in any other *Haplochromis* from Lake Victoria. Specimens with thickened but non-lobed lips have more broadly rounded dental arcades, which are, nevertheless, more acutely rounded anteriorly than those of most other species. Complete intergradation exists between the various arcade shapes; the correlation between lip development and dental pattern is not complete since some fishes with lobed lips have a broad arcade.

In fishes 70–108 mm. standard length the outer tooth row is composed of unicuspid and weakly bicuspid, slender and slightly recurved teeth. In larger individuals these teeth are always unicuspid, are stouter and very slightly, if at all, curved. From 16 to 46 teeth may occur in the outer series of the upper jaw; there is apparently some correlation between lip development and the number of teeth, with a tendency for lobe-lipped fishes to have more teeth.

The inner series are composed of tricuspid and weakly tricuspid teeth in fishes less than 110 mm. standard length, and of predominantly unicuspid teeth in larger individuals. These teeth are arranged in two or three rows (less commonly four or one) anteriorly in each jaw.

Lower pharyngeal bone triangular, the dentigerous area 1·0–1·5 (modal range 1·2–1·3) times as broad as long. With one exception, all specimens have the median teeth (particularly the posterior few pairs) enlarged but still clearly cuspidate. In the exceptional specimen, the median teeth are slender.

Coloration in life: Breeding males. Ground colour greyish-black or black; lips and branchiostegal membrane black. Dorsal fin black, lappets and margin of soft part red, as are the maculae between the branched rays. Caudal black basally, but light yellow or hyaline distally ; anal yellow or hyaline, with three or four reddish-yellow ocelli ; pelvics black. *Non-breeding males* : Ground colour variable, usually greyish-black ; a dark mid-lateral band and a less intense, interrupted, wavy dorsal band, are generally visible. Dorsal, caudal and anal fins greyish ; pelvics black.

Females and immature males. Ground colour greyish-silver, creamy-white on the chest and ventral surface of the head. Lips grey or cream ; six to nine dark transverse bars on the flanks and caudal peduncle, which are broadest at the points of intersection with the broad, mid-lateral stripe and the narrower, interrupted dorsal band. Dorsal caudal and anal fins greyish ; pelvics hyaline.

One of the eight females available was a piebald, black and yellow " *bicolor* " variant (p. 212) ; it was of the group with hypertrophied and lobed lips.

Preserved material : Sexually active males. Ground colour blackish, lower jaw, branchiostegal membrane and chest dusky ; lips usually pale but dusky in a few specimens. A dark, mid-lateral stripe and a less intense dorsal band, together with six or seven broad transverse bars, are usually visible on the flanks. Dorsal fin black, with light lappets and margin to the soft part. Anal fin pale orange-yellow, with three or four white ocelli arranged in a single row. Caudal fin black on the basal third to half, orange-yellow distally. Pelvic fins black, somewhat lighter medially. *Sexually inactive males* have a similar coloration except that the ground colour is lighter, as is the lower jaw and the branchiostegal membrane, whilst the chest is silvery. *Females and juvenile males* are brownish-fawn, lightest ventrally ; the banding and barring is more obvious than in adult males. All fins hyaline, with the soft part of the dorsal fin and the caudal fin maculate.

Distribution. Known from Lake Victoria and probably also from the Victoria Nile since the type locality is given as " Victoria Nile at Ripon Falls " (Boulenger, 1911).

Ecology : Habitat. H. chilotes is apparently confined to the littoral and sublittoral zones of the lake, where the depth of water is less than 50 feet and to localities with a hard substrate (sand, shingle and rocks). Only two specimens were caught over a mud bottom. Furthermore, it seems that the species may be confined to sheltered bays and gulfs ; with two exceptions, no *H. chilotes* have been recorded from exposed habitats. The exceptional fishes were caught near islands lying some distance from the mainland.

Food. Eight of the 23 specimens contained food in the stomach and intestines ; these fishes represent five different localities, four of which are geographically distant from one another.

One fish had fed almost exclusively on prawns (*Caridina nilotica* Roux) and the others on insect larvae. Larvae of the boring may-fly (*Povilla adusta* Navás) formed the main insect prey, and it was noticed that the silk case of the larva had also been ingested. Other insects eaten included Trichoptera and Diptera larvae. From the amount of plant debris and sand occurring in the stomach it would seem that *H. chilotes* feeds from the bottom.

Breeding habits. Females 70 mm. S.L. are sexually active, but the smallest adult male in this sample was 97 mm. S.L.; from the available data it seems probable that males reach a greater adult size than females. One female was found with three late larvae in the buccal cavity ; since the condition of this fish was clearly " spent " it is assumed that the larvae were part of a larger brood which was lost when the female was captured.

Morphology of late larval H. chilotes. The three young fishes (all *ca.* 10 mm. S.L.) referred to above are indistinguishable from the larvae of other and unrelated *Haplochromis* species. Although the female parent had hypertrophied and lobed lips, no trace of these characters was visible in the larvae.

Affinities. Haplochromis chilotes was probably derived from an *H. chromogynos*-like ancestor by further development of the lips, narrowing of the head and the consequent effects on the dental pattern. *H. chilotes* without lobed lips resemble *H. chromogynos* more closely than do specimens with lobed lips. But the similarity between the two species, even at its closest, is less marked than for example, that between *H. sauvagei* and *H. prodromus* (Greenwood, 1957).

There is a striking superficial resemblance between *H. chilotes* and *Lobochilotes labiatus* (Blgr.) of Lake Tanganyika. The range of lip development in *L. labiatus* is about equal to that of *H. chilotes* but with this difference ; it is positively correlated with size in *L. labiatus*. Small fishes have weakly lobed lips whilst, in larger individuals the lobes are well developed. Tooth form in *Lobochilotes* is quite unlike that of *H. chilotes*, but there is a tendency for the dental arcade to be acutely rounded anteriorly.

Lobed lips are also developed in *Haplochromis lobochilotes* of Lake Nyasa and thus there is some resemblance between this species and *H. chilotes*. In this instance, however, the similarity is less marked because the general proportions of the two species are somewhat different ; again, the form of the teeth is dissimilar.

Of the lobe-lipped species occurring outside Lake Victoria, *Melanochromis labrosus* Trewavas, of Lake Nyasa shows the greatest overall and detailed likeness with *H. chilotes*. The dentition of *M. labrosus* and *H. chilotes* of a comparable size is similar, as is the gross and finer morphology of the head. The nuchal and pectoral squamation of *M. labrosus* is, however, markedly smaller than that of *H. chilotes*. Unfortunately, *M. labrosus* is known only from one specimen so a detailed comparison of the two species cannot be made.

Diagnosis. H. chilotes with hypertrophied and lobed lips are immediately distinguishable from other Lake Victoria species on this character alone ; from *H. lobochilotes* of Lake Nyasa and *Lobochilotes labiatus* of Lake Tanganyika, it is distinguished by differences in the shape of the teeth and by various morphometric characters *Haplochromis chilotes* with moderately developed and weakly or non-lobed lips may be confused with *H. chromogynos* or with species of the *H. sauvagei* complex. They are immediately distinguishable from the latter group in having fewer rows of inner teeth and by the shape of the outer teeth, which do not have strongly recurved tips. From *H. chromogynos*, *H. chilotes* is distinguished by its narrower interorbital region and longer snout.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
Genoa Museum (Type *Paratilapia chilotes*)	Jinja, Ripon Falls	Bayon.
B.M. (N.H.).—1911.3.3.33 (Paratype *P. chilotes*)	,, ,,	,,
,, 1958.1.16.3	Ramafuta Is.	E.A.F.R.O.
,, 1958.1.16.4	Pilkington Bay	,,
,, 1958.1.16.5	Lukula Is.	,,
,, 1958.1.16.6	Channel between Dagusi Is. and mainland	,,
,, 1958.1.16.9	Ekunu Bay	,,
,, 1958.1.16.10–16	Off south tip of Buvuma Is.	,,
,, 1958.1.16.17–23	Napoleon Gulf, near Jinja	,,
	Tanganyika	
,, 1958.1.16.1	Kaseiraji Is.	,,
,, 1958.1.16.8	Godziba Is.	,,
	Kenya	
,, 1958.1.16.2	Kisumu Harbour	,,
	Lake Victoria, Locality Unknown	
,, 1958.1.16.7	—	,,

Haplochromis chromogynos sp. nov.

Haplochromis bicolor Blgr. (part), 1906, *Ann. Mag. nat. Hist.* (7) **17**, 444.
Paratilapia bicolor (Blgr.) (part), Blgr., 1915, *Cat. Afr. Fish.* **3**, 346.
Haplochromis sauvagei (Pfeff.), (part), Regan, 1922, *Proc. zool. Soc. London*, 167.

Haplochromis chromogynos is unique amongst the *Haplochromis* of Lake Victoria (and probably the other lakes as well) since a high percentage, if not all, of the females have a piebald, black and yellow " *bicolor* " coloration. " *Bicolor* " female variants are known to occur in several *Haplochromis* species, but in none does the frequency of the variants exceed about 30 per cent. All 22 specimens of female *H. chromogynos* are " *bicolor* ". These fishes were collected from several different parts of the lake and include fishes at various stages of sexual development.

Holotype. A female, 79 mm. standard length, from the Napoleon Gulf, near Jinja, Uganda.

Description, based on 29 specimens (including the holotype) 50–110 mm. standard length.

Depth of body 32·5–42·3 (M = 35·0) per cent of standard length ; length of head 30·4–37·3 (M = 33·2) per cent. Dorsal head profile curved and moderately declivous. Preorbital depth 13·2–17·0 (M = 15·4) per cent of head length, least interorbital width 22·6–31·4 (M = 27·5) per cent. Snout slightly longer than broad, or less commonly, broader than long, its length 26·3–33·3 (M = 30·7) per cent of head ; eye 25·7–32·7 (M = 28·6) ; depth of cheek 17·9–24·6 (M = 21·6) per cent of head.

Caudal peduncle 13·6–18·5 per cent of standard length, 1·1–1·6 times as long as deep.

Mouth horizontal; jaws equal anteriorly, the lower 1·1–1·5 (mode 1·3) times as long as broad, its length 30·0–34·4 (M = 32·5) per cent of head length. Lips thickened; posterior tip of the maxilla extending to the vertical through the anterior orbital margin or slightly beyond.

Gill rakers short, 8 (less frequently 9 and rarely 6 or 7) on the lower limb of the anterior arch.

Scales ctenoid; lateral line with 31 (f.3), 32 (f.10), 33 (f.13) or 34 (f.3) scales. Cheek with 3 (less frequently 2 or 4) series. Six to 8 scales between the origin of the dorsal fin and the lateral line; 8 or 9 between the pectoral and pelvic fin bases; chest scales small.

Fins. Dorsal with 24 (f.3), 25 (f.24) or 26 (f.2) rays, anal with 11 or 12, comprising XV–XVI, 8–10 and III, 8 or 9 spinous and branched rays for the fins respectively. Pectoral fin slightly shorter than the head; first pelvic ray produced, variable in its posterior extension but usually reaching the spinous part of the anal fin.

Teeth. In the outer row of both jaws, the teeth are slender and gently recurved. Fishes less than 65 mm. S.L., have only unequally bicuspid teeth; individuals 65–95 mm. S.L. have an admixture of bi- and unicuspid teeth in which either type may predominate. Fishes more than 95 mm. S.L. have only unicuspid teeth. There are 24–42 (modal range 30–32) outer teeth in the upper jaw.

The inner teeth are tricuspid in fishes less than 95 mm. S.L. and unicuspid in larger individuals; an admixture of both types may occur. These teeth are arranged in three rows (less frequently two or four) in both jaws.

Lower pharyngeal bone triangular, the dentigerous area 1·1–1·4 (mode 1·2) times as broad as long. Occasionally the median series of teeth are enlarged and submolariform; more frequently, only the posterior few pairs are markedly enlarged. In a few specimens, no median teeth are enlarged.

Coloration. As mentioned above, *H. chromogynos* is unique in apparently having only "*bicolor*" females. The colour patterns of these fishes are variable, but are within the range known for other species with "*bicolor*" females. In preserved material, the yellowish-silver ground colour appears yellowish-white, silver or brown. *The colours of live males* are unknown.

Coloration of preserved males. Ground colour greyish-brown to grey; lips, lower jaw and the anterior part of the branchiostegal membrane, lighter; six or seven faint transverse bars visible on the flanks and caudal peduncle; a faint lachrymal stripe is often present. Dorsal fin with the spinous part dusky, lappets lighter; soft part orange-yellow. Anal dusky on the basal half, orange-yellow distally, with one to three white ocelli arranged in a single row. Caudal fin dark, but with a broad, orange-yellow margin. Pelvic fins black on the outer half, orange mesially.

Ecology: Habitat. H. chromogynos is probably confined to the littoral zone and to water less than 20 feet deep; it has only been caught over a firm substrate (rock, sand or shingle).

Food. One record of stomach and intestinal contents is available; the main contents were the remains of Trichoptera larvae and sand-grain cases, but a few larval chironomids and baétids were also identified.

Breeding. One female carrying embryos in the buccal cavity was recorded. Sexual maturity is reached at a standard length of 90–100 mm. in both sexes.

Affinities. H. chromogynos may be related to *H. chilotes* (see p. 211). The similarity between these species is most pronounced when the non-lobed lip forms of *H. chilotes* are compared with *H. chromogynos.* Superficially, *H. chromogynos* resembles *H. crassilabris* (Blgr.) but the dentition of the two species is markedly different.

The available specimens of *H. paucidens* Regan, from Lake Kivu, indicate a very close relationship between the two species ; the most marked difference is the shallower cheek of *H. chromogynos* (mean depth 21·6, cf. 27·6 per cent for *H. paucidens*). Unfortunately there is no information on the coloration of female *H. paucidens* or on the breeding colours of male fishes of either species.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1958.1.16.83 (Holotype)	Napoleon Gulf, near Jinja	E.A.F.R.O.
,, 1958.1.16.71–75	Napoleon Gulf, near Jinja golf course	,,
,, 1958.1.16.76–81	Napoleon Gulf, Jinja pier	,,
,, 1958.1.16.82	Napoleon Gulf, bay opposite Jinja pier	,,
,, 1958.1.16.84	Entebbe Harbour	,,
,, 1958.1.16.69	Grant Bay	,,
,, 1958.1.16.67–68	Ramafuta Is., Buvuma Channel	,,
,, 1906.5.30.415–416	Bugangu	Degen.
,, 1906.5.30.407–412	Bunjako	,,
	Tanganyika	
,, 1958.1.16.63–66	Mwanza, Capri Bay	E.A.F.R.O.
	Kenya	
,, 1958.1.16.70	Kisumu Harbour	,,

Haplochromis aelocephalus sp. nov.

(Text-fig. 12)

Holotype. A male 96 mm. S.L., from Igwe Island.

An interesting feature of this species is its wide range of variation in head shape ; the more extreme individuals might well be considered distinct species were it not for the presence of annectent forms (Text-fig. 13). This variation is not correlated with sex or size. The most constant specific characters are the multiseriate dentition, the small scales on the pectoral region, and the thickened lips.

Description. Based on the holotype and 21 other specimens, 63–120 mm. standard length.

Depth of body 31·3–38·4 per cent of standard length ; length of head 33·0–38·6 per cent. Dorsal head profile straight or very slightly concave, sloping gently ; physiognomy variable. Preorbital depth 14·7–19·4 (M = 17·2) per cent of head length, least interorbital width 21·9–26·4 (M = 24·8) per cent. Snout 1·1–1·2 times as long as broad, except in a few extreme individuals where it is 1·25–1·30 times as long as broad; snout length 32·0–39·0 (M = 35·3) per cent of head. Diameter of eye shows fairly clear-cut negative allometry with standard length, 25·0–30·8 (M = 27·8) per cent of head in fishes 62–100 mm. S.L. and 23·2–25·7 (M = 24·5) per cent in larger individuals; depth of cheek 17·3–24·7 (M = 20·5) per cent.

Caudal peduncle 12·8–18·5 (M = 16·2) per cent of standard length, 1·1–1·6 (modal range 1·4–1·5) times as long as deep.

Mouth horizontal, lower jaw projecting slightly; posterior tip of the maxilla not quite reaching the vertical through the anterior margin of the orbit, except in one specimen. Lips thickened and variable; in a few fishes there are faint indications of a lobe-like swelling on the lower lip. In all specimens there is a pronounced submental thickening which extends posteriorly for a short distance. Lower jaw length apparently correlated with head shape, being greatest in the more extreme individuals; namely, in seven " extreme " specimens (Text-fig. 13) 42·5–48·5 (M = 45·1) per cent of head and in the remaining specimens 37·0–46·9 (M = 41·3) per cent. The length/breadth ratio of the lower jaw 1·6–2·6 (modal range 1·8–2·0).

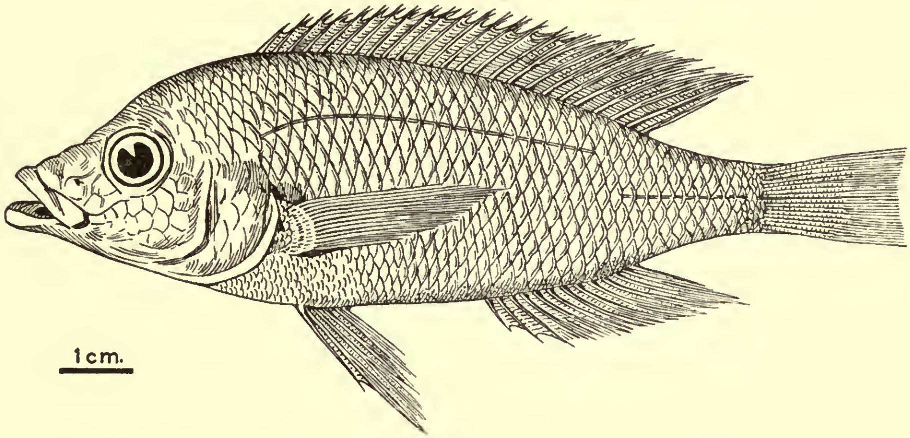

FIG. 12. *Haplochromis aelocephalus*; holotype. Drawn by Miss D. Fitchew.

Gill rakers short, 7–9 on the lower limb of the anterior arch.

Scales ctenoid; lateral line with 31 (f.1), 32 (f.5), 33 (f.10) or 34 (f.6) scales. Cheek with 3 or 4 (rarely 2) series. Six to 8 scales between the origin of the dorsal fin and the lateral line; 8 or 9 (rarely 7 or 10) scales between the pectoral and pelvic fin bases; chest scales small.

Fins. Dorsal with 24 (f.3), 25 (f.17) or 26 (f.2) rays, anal with 11 (f.1), 12 (f.16) or 13 (f.5), comprising XV or XVI, 9 or 10 and III, 8–10 spinous and branched rays for the fins respectively. Pelvic fins with the first ray produced. Pectoral fin shorter than the head. Caudal truncate or subtruncate.

Teeth. The outer row in both jaws of fishes less than 65 mm. S.L. is composed of slender and slightly recurved bicuspid teeth; specimens 65–95 mm. S.L. have an admixture of bi- and unicuspids in which either form may predominate, whilst in larger fishes, all the outer teeth are unicuspid. There are 24–42 (mode 32) teeth in the outer row of the upper jaw. The dental arcade in the lower jaw is narrow anteriorly; in a few specimens it is rather acutely pointed and resembles that of lobe-lipped *H. chilotes* (see p. 209).

Teeth in the inner series of both jaws are generally tricuspid in fishes less than 95 mm. S. L. and unicuspid in larger individuals; a mixture of both types is found in specimens of an intermediate size. There are three to five, rarely two (mode five), series of inner teeth anteriorly in the lower jaw and three to six (mode five) in the upper. The innermost series of the lower jaw is usually implanted so as to lie almost horizontally.

Lower pharyngeal bone triangular, the dentigerous area 1·0–1·4 (mode 1·2) times as broad as long. Teeth in the median series are variable in form. In most specimens these teeth (especially the upper three or four pairs) are somewhat enlarged and weakly cuspidate; the next most common variant has these teeth slightly enlarged and clearly cuspidate. Finally, in a few fishes the median teeth are unmodified and resemble the other teeth. Two exceptional fishes had the entire median series enlarged and molariform and the pharyngeal bone noticeably stouter.

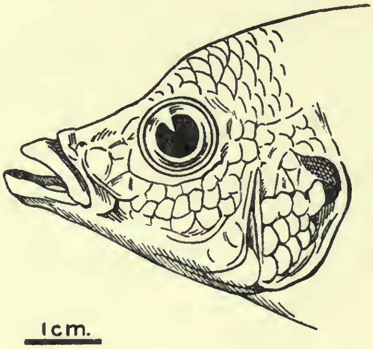

FIG. 13. *Haplochromis aelocephalus*; individual variant of head profile (extreme form).

Coloration. The colours of living fishes are unknown.

Preserved material: Sexually active males. Ground colour grey-black, chest and branchiostegal membrane black; faint indications of a coppery sheen on the operculum and flanks. Dorsal fin black except for the light lappets and a colourless band outlining the soft part of the fin; caudal black basally, light (? orange) distally; anal fin dark on the basal half and light (? orange) distally, with three or four hyaline ocelli arranged in a single row. Pelvics black. *Females, quiescent and juvenile males*. Ground colour greyish-silver (in sexually quiescent males there is a faint trace of coppery sheen on the operculum and the chest is dusky) with, in some, an interrupted or continuous, dark, mid-lateral stripe and five or six transverse bars on the flanks. Dorsal and anal fins yellowish, slightly dusky on the proximal half in quiet males, but hyaline and faintly maculate in females and immature males. Pelvic fins yellowish or hyaline in females and immature males, dusky in quiet males.

Distribution. Known only from Lake Victoria.

Ecology : Habitat. The species has been found in relatively few localities and only in the Uganda waters of the lake. However, the available data suggest that *H. aelocephalus* is restricted to water less than 40 feet deep and to areas where the substrate is firm (sand and rock).

Food. Sixteen of the 20 specimens examined had food in the stomach or intestines ; from these it would seem that *H. aelocephalus* preys on a variety of invertebrate animals, and possibly even small fishes.

In ten specimens the predominant food organisms were insects (particularly dipterous larvae, but also Ephemeroptera [*Povilla adusta*] and Trichoptera larvae). The non-insect food identified was : in two fishes, oligochaet worms ; in one, the remains of a prawn (*Caridina nilotica* Roux) ; in another, fragments of plant-tissue and a few Ostracoda ; and in two others, numerous fragments of lamellibranch and gastropod shells. One exceptional individual contained the remains of a small cichlid fish.

The presence of sand grains in the stomach and intestines of many individuals suggests that the species may be a bottom feeder.

Breeding. No data are available.

Affinities. Haplochromis aelocephalus shows no special affinity with any other *Haplochromis* species in Lake Victoria ; the less extreme individuals resemble members of the *H. nigrescens* species-complex of piscivorous-insectivorous predators. The multiseriate dentition, however, disqualifies *H. aelocephalus* from a place in this complex, but suggests relationship with species of the *H. sauvagei-H. prodromus* group, and particularly *H. xenognathus.* In shape, the teeth of *H. aelocephalus* are unlike those of *H. xenognathus* which have characteristically recurved tips (Greenwood, 1957). In certain cephalic characters, especially the shape of the lower jaw, the narrow lower dental arcade and the semi-lobate lips, *H. aelocephalus* approaches *H. chilotes* but in all other characters there is no obviously close relationship between the two species.

Diagnosis. H. aelocephalus may be distinguished by the following combination of characters : proportions of the head ; a multiseriate dentition with the outer teeth slender and gently recurved ; lips somewhat thickened.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.)—1958.1.16.244 (Holotype)	Igwe Isl.	E.A.F.R.O.
,, 1958.1.16.215	Ekunu Bay	,,
,, 1958.1.16.216	Entebbe, Bugonga Beach	,,
,, 1958.1.16.217	Beach near Nasu Point, Buvuma Channel	,,
,, 1958.1.16.218–224	Igwe Isl.	,,
,, 1958.1.16.225–228	Bay opposite Jinja, Napoleon Gulf	,,
,, 1958.1.16.232–233	Pilkington Bay	,,
,, 1958.1.16.234–235	Buka Bay	,,
,, 1958.1.16.236–242	Napoleon Gulf, near Jinja	,,
,, 1958.1.16.243	Unknown	,,

SUMMARY

1. Seven species, which feed almost exclusively on the embryos and larvae of other Cichlidae, are discussed. *Haplochromis obesus* (Blgr.), *H. maxillaris* Trewavas, *H. melanopterus* Trewavas, *H. parvidens* (Blgr.) and *H. microdon* (Blgr.) are redescribed on the basis of new and more extensive collections. Two new species, *H. cronus* and *H. cryptodon* are described.

2. Notes on the ecology and feeding habits of these species are given.

3. The relationships of these species are discussed and it is concluded that the group has a polyphyletic origin.

4. Four other species are considered. These are all insectivorous and do not appear to be closely related to the other species of *Haplochromis* in Lake Victoria. *Haplochromis plagiodon* Regan & Trewavas and *H. chilotes* (Blgr.) are redescribed, and two new species, *H. chromogynos* and *H. aelocephalus* are described.

5. *H. chromogynos* is of particular interest since the normal female coloration is apparently the "*bicolor*" piebald which occurs as an infrequent and sex-limited mutant amongst the females of other and unrelated species.

6. Both *H. chilotes* and *H. aelocephalus* are noteworthy for the wide range of individual variability which they show.

ACKNOWLEDGMENTS

I wish to acknowledge my gratitude and thanks to the Trustees of the British Museum (Natural History) for the facilities afforded me; to the authorities of the Muséum National d'Histoire naturelle, Paris and of the Museo Civico di Storia Naturale, Genoa, who graciously allowed me to study type-material in their collections; and to Mr. A. C. Wheeler of the Zoology Department, British Museum (Natural History) who was responsible for making several radiographs used in this study. I am especially indebted to Dr. Ethelwynn Trewavas for her most helpful advice and criticism.

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26 FEB 1959

THE *ROSAURA* EXPEDITION
1937-38
CHAETOGNATHA

JOHN S. COLMAN

BULLETIN OF
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ZOOLOGY Vol. 5 No. 8
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Pp. 219-253

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THE *ROSAURA* EXPEDITION 1937-38
CHAETOGNATHA

By JOHN S. COLMAN

INTRODUCTION

Genus ***SAGITTA*** Quoy & Gaimard, 1827

Group	Species	Number	Number of hauls
(a) " *Friderici* "	1. *Sagitta friderici* Ritter-Záhony, 1911	2	2
	2. *S. tenuis* Conant, 1896	177	2
(b) " *Bipunctata* "	3. *S. bipunctata* Quoy & Gaimard, 1827	6	5
	4. *S. elegans* Verrill, 1873	42	2
	5. *S. robusta* Doncaster, 1902	14	3
(c) " *Serratodentata* "	6. *S. serratodentata* Krohn, 1853	95	4
(d) " *Lyra* "	7. *S. lyra* Krohn, 1853	110	11
	8. *S. maxima* (Conant, 1896)	167	10
(e) " *Hexaptera* "	9. *S. hexaptera* d'Orbigny, 1843	299	11
	10. *S. decipiens* Fowler, 1905	29	7
(f) " *Enflata* "	11. *S. enflata* Grassi, 1881	141	13
(g) " *Planctonis* "	12. *S. planctonis* Steinhaus, 1896	12	2
	13. *S. zetesios* Fowler, 1905	84	10
(h) Ungrouped	14. *S. neglecta* Aida, 1897	7	5
	15. *S. pulchra* Doncaster, 1902	2	1
	16. *S. macrocephala* Fowler, 1905	107	7
	Genus ***PTEROSAGITTA*** Costa, 1869		
	17. *Pterosagitta draco* (Krohn, 1853)	45	9
	Genus ***KROHNITTA*** Ritter-Záhony, 1910		
	18. *Krohnitta subtilis* (Grassi, 1881)	11	5
	Genus ***EUKROHNIA*** Ritter-Záhony, 1909		
	19. *Eukrohnia hamata* (Möbius, 1875)	204	5
	20. *E. fowleri* Ritter-Záhony, 1909	277	9
	Total	1831	19

THIS collection contains 1,831 individuals of 20 species (16 of *Sagitta*, 1 *Pterosagitta*, 1 *Krohnitta* and 2 *Eukrohnia*) taken in 19 hauls. In the above list the order of species and the groups of *Sagitta* are based on Furnestin (1957); I have added the group "*planctonis*" (see David, 1956). The most distinct of these groups, such as "*lyra*" and "*planctonis*", are undoubtedly of some value in making minor distinctions within the genus *Sagitta*, but no useful purpose would be served by raising them to subgeneric rank; it would be only a matter of time before attempts would be made to raise such subgenera to generic status, and this would only create confusion.

The full list of stations on the *Rosaura* expedition is given in Colman (1954).

I am grateful to Dr. J. H. Fraser, Dr. E. L. Pierce and Mr. P. M. David for much helpful and interesting correspondence. Dr. Pierce and Mr. David both examined some of my specimens and sent me some of theirs, and Dr. Fraser kindly read through the typescript. I also wish to thank Dr. Ben Dawes for examining the parasites.

Before the catches of chaetognaths are discussed in detail, the limitations of this collection should be pointed out. All the catches were made with open nets, so that in the case of the deep hauls there is no telling in most cases from what depth the specimens came. With one exception, all the deep hauls were made with a 2-metre stramin net; the stramin mesh is too coarse for the reliable sampling of the smaller and more slender species, such as *S. friderici*, *S. tenuis*, *S. bipunctata*, *S. robusta*, *S. serratodentata*, *S. decipiens*, *S. neglecta*, *S. pulchra*, *P. draco* and *K. subtilis*, all of which were probably under-represented in the deep hauls.

Each deep haul lasted about two hours, and each catch contained up to hundreds of fish and scores of molluscs, crustacea etc., many of which were larger than the chaetognaths. Sorting was done single-handed; all that I was able to do was to pick out specimens of about 30 different categories in the various phyla until I did not appear to be finding anything new. It is hoped that this procedure will give some idea of the relative abundance at each station of at any rate the larger chaetognaths, but I do not think that I sampled adequately such smaller species as the stramin net was able to retain.

Within the chaetognaths themselves the only sorting done on the spot was between red and colourless forms. All of *Sagitta macrocephala* and *Eukrohnia fowleri* were red, and there were occasional red individuals of *S. enflata*, *S. zetesios* and *Pterosagitta draco*.

Owing to the length of the deep hauls, many of the specimens are more or less damaged; this is much less true of the short hauls made near the surface with the small silk townet, which confirms the observation of David (1955, p. 240). In addition, all my samples (after killing with formalin) were preserved in 70% alcohol; weak sea-water formalin should have been used, since alcohol encourages contraction and leads to damage. These factors have combined to make useless in many cases such taxonomically valuable structures as seminal vesicles, corona and fins, and to make many of my length-measurements of only relative value. Length-measurements in any case should be treated with some caution; Russell (1932*a*, *b*; 1933*a*, *b*) and Clarke *et al.* (1943) have shown that there is a very considerable difference in length between successive broods of *Sagitta elegans* and *S. setosa* at different times of the year, and the same may well be true of other species which have not been studied with equal thoroughness.

The hauls could not be planned much in advance, but were made when time and depth permitted. The depth of the net was calculated roughly from a visual estimation of the angle of the towing warp to the horizon, and cannot pretend to be accurate. It was my intention, at each haul, to send the net to a depth of about 1,000 m., but several hauls had to be shallower than this; sometimes there was not time to pay out and haul in enough wire, and sometimes there was no nearby sounding on the chart and the possible existence of sea-mounts had to be borne in mind.

With the exception of the very young *Sagitta elegans* in Stations 4 and 7, every specimen has been examined for the following features:

Overall length to the nearest 0·1 mm. (excluding tail fin) measured on a glass slide graduated in half-millimetres (some of the smallest were measured by eye to 0·05 mm.).

Length of tail, expressed as percentage of total length.

Numbers of hooks, of *anterior teeth* and of *posterior teeth*; whenever the two sides differed the larger number was taken, and I have included the smallest visible hook-rudiments.

State of development of gonads. Several not dissimilar schemes exist for classifying the developmental stages of chaetognaths, notably those of Kramp (1917, 1939), Russell (1932), Thomson (1947), Faure (1953) and David (1955). The arbitrary division into stages of a continuous process is bound to be to some extent subjective so it is desirable for each author to define the stages which he uses. I have recorded the state of development of my specimens in six stages, as follows:

Stage O: neither testes nor ovaries visible under × 100 magnification.
,, I: testes visible, but no sperm-balls or spermatozoa free in tail coelom; ovaries visible but very small.
,, II: tail filled with spermatozoa, ovaries developing but eggs small.
,, III: tail empty, ovaries further developed, with some eggs larger than others; some eggs may even be full-sized.
,, IV: tail empty; all eggs full-sized; in some cases, probably because of damage, many eggs are free in the trunk coelom.
,, V: spent, the ovaries being reduced to crumpled remnants.

Stage V seems to be almost confined to the genus *Eukrohnia*. This seems to imply that most, if not all, species of *Sagitta* die very soon after ovulation (or after the last ovulation in species such as *S. enflata* which are believed to go through more than one reproductive cycle in a lifetime). Indeed, van Oye (1931) states that this is so.

The relative duration of the several stages, the speed of transition from one stage to the next, and the relative speed of development of testes and ovaries, vary not only between one species and another, but also to some extent between individuals of one species. I have occasionally found it convenient (especially in the case of *Sagitta lyra*, see below) to record two intermediate stages.

Stages I–II: testes still retaining their shape, but some sperm-balls already free in tail coelom.
“ II–III: some spermatozoa still in tail, but ovaries quite as mature as in some specimens of stage III.

DEEP-WATER HAULS

Thirteen plankton hauls were made in deep water with 2-metre nets, 12 with the stramin net and one (Station 14) with a silk net of quarter-inch mesh. The latter net, as might be expected, caught very few chaetognaths, and one of the stramin net hauls (Station 41) was spoilt by containing a large shark. The details of the samples from these stramin net hauls are shown in Table I.

Station 8 was in near-Arctic waters south-west of Greenland, Station 13 was in temperate waters between the Gulf Stream and the continental shelf off the eastern United States, and the remainder were in tropical waters ; Stations 15–33 were in the Caribbean Sea, and Stations 42–46 in the central Atlantic. Station 8 took place at night ; all the others were in daylight.

The sample from Station 8 can be compared with the catches from the *Godthaab* Expedition of 1928, described by Kramp (1939). In deep water south-west of Cape Farewell Kramp found that *Sagitta maxima* and *Eukrohnia hamata* were abundant, with " *S. planctonis* " (= *S. zetesios*) (see David, 1956) and *E. fowleri* less common. In *Rosaura* Station 8 the same four species occurred in the same order of abundance, but to them can now be added the red, deep-water species, *S. macrocephala*. It is surprising that Kramp found none of the latter species. for the *Godthaab's* hauls were made at all depths down to 2,000 m., a good deal deeper than mine which I estimated to reach 1,300 m.

A submarine ridge joins southern Greenland to southern Baffin Land about 65° N. According to Kramp neither " *Sagitta planctonis* " (= *S. zetesios*) nor *Eukrohnia fowleri* is found north of the ridge. *S. maxima* and *E. hamata*, however, both extend northwards as far as Ellesmere Land and North Greenland, and in these northern waters they are joined by *S. elegans arctica* as an offshore species. Further south in the Davis Straits the latter species is confined to inshore waters ; I found no *S. elegans* in Station 8, but did catch some very young juveniles (Stage O) in Stations 4 and 7 near the Greenland coast.

Station 13 was taken about 60 miles north-east of Cape Hatteras, and was thus only just outside the area covered by Pierce (1953). To judge by the surface temperature (17·8° C.) and the fact that the ship was being set to the southward, Station 13 must have been in the " slope " water between the Gulf Stream and the continental shelf, and the position would correspond roughly to Pierce's " Outer Shelf Zone ". Pierce recorded 11 species from this zone, and I identified eight species from the sample in Station 13, but only three species are common to the two lists, namely *Sagitta enflata*, *S. lyra* and *S. bipunctata*, as is shown on p. 225.

The five species in the *Rosaura* sample which were missing from Pierce's list all inhabit moderately deep or deep water ; few of Pierce's samples came from deeper than 200 m. Of the eight species in Pierce's list which were not found in Station 13, seven are small species which would not be caught in large numbers by a stramin net (though most of them did appear from time to time in other *Rosaura* samples). The remaining one, *S. hexaptera*, is a large species which throughout the Caribbean and the central Atlantic was one of the most regularly occurring in the *Rosaura* samples, and was often the most numerous. Pierce records it as " rare " in the Cape

Species	Pierce (1953) Outer Shelf Zone (+++, common ++, occasional +, rare)	*Rosaura* Station 13 (Numbers in sample)
Sagitta minima	+++	..
S. serratodentata	+++	..
S. helenae	+++	..
S. tenuis	++	..
S. hexaptera	+	..
Krohnitta pacifica	+++	..
K. subtilis	+	..
Pterosagitta draco	+++	..
Sagitta enflata	+++	14
S. lyra	+	2
S. bipunctata	+++	1
S. maxima	..	12
S. zetesios	..	5
S. macrocephala	..	4
Eukrohnia hamata	..	51
E. fowleri	..	14

Hatteras-Cape Fear region, and it has been occasionally recorded from as far north as Nova Scotia (Pierce quotes Huntsman, 1919); its absence from *Rosaura* Station 13 may indicate that it is common only to the southward of Cape Hatteras.

At Station 8 the surface temperature was 4·8° C., and at Station 13, 17·8° C. All the other offshore hauls with the stramin net were made in tropical waters with the surface temperatures ranging from 25·5 to 28·3° C., and throughout the extensive area from Central America to the eastern central Atlantic the catches on the whole resembled one another closely.

Of the species large enough not to be able to escape through a stramin net, *Sagitta hexaptera, S. enflata, S. maxima, S. lyra* and *S. zetesios* occurred regularly in all or nearly all of the samples, and of these *S. hexaptera* was usually the most abundant. *S. maxima,* though usually present, seems to have been distinctly scarcer in tropical waters than in the Davis Straits (Station 8).

Another sizeable species, *S. planctonis,* was found only in the samples from the two easternmost stations (45 and 46) between St. Paul's Rocks and the west coast of Africa, as was the smaller and more slender *S. friderici*. *Eukrohnia hamata,* which dominated the catches in the two most northerly stations (8 and 13), was scarce in the tropics, providing only 14 specimens in three out of nine hauls.

Of the smaller species, *Sagitta decipiens* and *Pterosagitta draco* occurred with surprising regularity and must have been abundant everywhere. The paucity of the other species does not necessarily indicate that they were rare; a stramin net would let most of them through, and my sampling technique was not adequate for such as were caught.

A special mention may be made of the two red species, *Sagitta macrocephala* and *Eukrohnia fowleri*. Of the nine tropical hauls, the estimated depth of the net was at least 1,000 m. in five of them, but not more than 900 m. in the other

TABLE I.—*Samples from Deep-water Hauls*

2-metre stramin net (except Station 14, 2 m. ½-in. net)

Station No.	Date	Lat.	Long.	Position	Depth of sea (by chart) (m.)	Surface temp. (°C.)	Approx. depth of net (m.)	*Sagitta friderici*	*S. bipunctata*	*S. robusta*	*S. serratodentata*	*S. lyra*	*S. maxima*	*S. hexaptera*	*S. decipiens*	*S. enflata*	*S. planctonis*	*S. zetesios*	*S. neglecta*	*S. pulchra*	*S. macrocephala*	*Pterosagitta draco*	*Krohnitta subtilis*	*Eukrohnia hamata*	*E. fowleri*	Total	Number of species
8	11.ix.37	58° 48′ N.,	46° 11′ W.	Off SW. Greenland	>2,750	4·8	1,300	—	—	—	—	—	85	—	—	—	—	15	—	—	19	—	—	139	6	**264**	5
13	10.x.37	36° 88′ N.,	74° 23′ W.	Off U.S.A. ? "Slope" water	>1,800	17·8	750	—	1	—	—	2	12	—	—	14	—	5	—	—	4	—	—	51	14	**103**	8
14	13.x.37	24° 53′ N.,	77° 40′ W.	Tongue of the Ocean (Bahamas)	c. 1,800	27·8	900	—	—	—	—	—	—	2	—	1	—	—	—	—	2	—	—	—	2	**7**	4
15	17.x.37	18° 21′ N.,	75° 25′ W.	Bet. Cuba and Jamaica	c. 1,800	28·3	1,250	—	—	2	—	11	—	43	3	16	—	—	1	—	—	4	2	1	7	**90**	10
27	8.xi.37	16° 22′ N.,	86° 40′ W.	West of Roatan Is., Hond.	?	?	600	—	—	7	—	19	7	51	13	33	—	9	3	—	—	1	4	—	—	**147**	10
28	12.xi.37	16° 44′ N.,	85° 42′ W.	N. of Bonacca Is. (Hond.)	c. 3,000	27·8	1,100	—	—	—	—	25	7	9	8	11	—	7	1	—	39	—	2	—	84	**193**	10
32	17.xi.37	12° 42′ N.,	80° 25′ W.	400 km. NNW. of Colon	c. 2,000	27·8	900	—	—	—	2	21	19	63	1	6	—	12	—	—	—	3	—	—	—	**127**	8
33	22.xi.37	11° 00′ N.,	75° 43′ W.	Off Puerto Colombia	c. 1,500	27·8	1,200	—	—	—	—	8	11	13	2	9	—	5	—	—	7	2	1	—	53	**111**	10
*41	18.xii.37	0° 38′ S.,	43° 42′ W.	Off. N. Brazil	2,050	26·1	900	—	—	—	—	1	—	—	—	9	—	1	—	—	—	—	—	—	—	**11**	3
42	21.xii.37	5° 51′ S.,	34° 38′ W.	Off NE. Brazil	2,594	26·5	1,200	—	1	—	—	4	5	44	1	4	—	4	—	2	24	1	—	7	34	**131**	12
43	27.xii.37	3° 35′ S.,	32° 20′ W.	19 km. N. of F. Noronha	c. 2,000	25·5	750	—	1	—	—	8	6	25	—	—	—	11	—	—	—	13	—	—	—	**64**	6
45	29.xii.37	4° 15′ N.,	26° 20′ W.	Equatorial current	c. 4,500	26·6	900	1	2	—	1	3	3	27	—	3	5	—	—	—	—	1	—	—	2	**48**	10
46	30.xii.37	7° 27′ N.,	23° 08′ W.	? Guinea current	c. 4,400	26·6	1,000	1	—	5	2	8	12	13	1	24	7	15	1	—	12	14	2	6	75	**168**	16
					Total			**2**	**5**	**14**	**5**	**110**	**167**	**290**	**29**	**130**	**12**	**84**	**6**	**2**	**107**	**39**	**11**	**204**	**277**	**1,464**	18
					Number of stations			2	4	3	3	11	10	10	7	11	2	10	4	1	7	8	5	5	9	13	—

* Catch spoilt through capture of 7-ft. shark.

TABLE II. *Samples from Inshore Hauls*

Small silk townet (about 60 meshes to 1 in.)

Station No.	Date	Lat.	Long.	Position	Depth of sea (m.)	Surface temp. (°C.)	Salinity (°/₀°)	Depth of net (m.)	*Sagitta tenuis*	*S. bipunctata*	*S. elegans*	*S. serratodentata*	*S. hexaptera*	*S. enflata*	*S. neglecta*	*Pterosagitta draco*	Total
4	3.ix.37	60° 35′ N.,	46° 45′ W.	Off Julianehaab, Grnld.	550	c. 5	—	20	—	—	34	—	—	—	—	—	**34**
7	9.ix.37	60° 17′ N.,	44° 37′ W.	Tasermiut Fjord, Grnld	35	c. 5	—	10	—	—	8	—	—	—	—	—	**8**
23	30.x.37	17° 29′ N.,	88° 10′ W.	Belize Hbr., Brit. Honduras	5	28·5	—	2–3	—	—	—	—	—	6	1	—	**7**
38A	8.xii.37	8° 15′ N.,	59° 45′ W.	Morowhana, Brit. Guiana	12	26	10·90	2	104	—	—	—	—	—	—	—	**104**
40	13.xii.37	6° 40′ N.,	58° 10′ W.	Georgetown, Brit. Guiana	7	26	13·9	2	73	—	—	—	—	—	—	—	**73**
44	28.xii.37	0° 56′ N.,	c. 29° W.	St. Paul's Rocks	10	26	—	2	—	1	—	90	9	5	—	6	**111**
								Total	**177**	**1**	**42**	**90**	**9**	**11**	**1**	**6**	**337**

four. *S. macrocephala* occurred in none of the latter, but provided 82 specimens in four of the deeper hauls; *E. fowleri* was represented by two specimens in one (900 m.) of the less deep hauls, but by 253 in all five of the deeper ones. This fairly sharp division between 900 m. and 1,000 m. may show that my estimates of net-depth are at any rate reasonably self-consistent.

INSHORE HAULS

Six short hauls were made near the surface with a small silk townet of about 60 meshes to the inch. The details of the samples from these are shown in Table II.

The first two of these hauls (Stations 4 and 7) were taken in Greenland coastal waters. The first was, it is true, over fairly deep water (550 m.), but the coast was less than 10 miles away, and the catch looked like inshore plankton, being dominated by medusae and ophioplutei. At Station 7 there were few plutei, but again medusae were conspicuous. The only chaetognaths in these catches were some very young (stage O) *Sagitta elegans*, presumably the subspecies *arctica*; since this species did not appear in the offshore sample at Station 8, these observations tend to confirm Kramp's (1939) statement that in the Davis Straits *S. elegans* is confined to coastal waters.

The catch at Station 23 in Belize Harbour (British Honduras) calls for little comment. It was made over shallow water in bright sunshine, and the few chaetognaths caught (one *S. neglecta* and six *S. enflata*) were all very young; the largest of the *S. enflata* was only 3·1 mm. long, and the others were post-larvae still with relatively very large ventral ganglia. The rest of the catch was typical of inshore waters, and was dominated by medusae, post-larval polychaetes, and the larvae of decapods and molluscs.

The next two hauls (Stations 38A and 40) are of considerable interest. They were both taken in the complex system of rivers and creeks in British Guiana where the water is very opaque (more so than the most turbid water in the Tamar Estuary, for example), the salinity low (10·9 and 13·9‰), and the plankton abundant, varied, and entirely marine in character. The most numerous groups in the plankton were young fish and fish larvae, penaeid prawns, copepods and chaetognaths, all of the last group being *Sagitta tenuis*. These tidal waterways are discussed at greater length by Colman & Cooper (1954), and *S. tenuis* will be considered below in the section devoted to the individual species.

The last silk net haul to contain any chaetognaths, Station 44, was made a few feet off St. Paul's Rocks, the tiny, isolated land-mass in the middle of the "waist" of the Atlantic. The shelf from which the rocks project is only a few hundred metres across and it supports a generous growth of algae, hydroids, polyzoa, sponges etc., accompanied by other invertebrates. At the time of the *Rosaura*'s visit the equatorial current was sweeping between the rocks from east to west at about 2 knots, but the plankton seemed to contain a local concentration of neritic forms, including mysids, orange, blue and variegated copepods, and post-larval gastropods. The five species of chaetognath, however, were all widely-distributed oceanic species; in the sample of 111 there were a single *Sagitta bipunctata*, several each of *S. hexaptera*, *S. enflata* and *Pterosagitta draco*, and 90 *S. serratodentata*.

This population is not unlike that in the surface waters at Fernando de Noronha, some 300 miles (500 kilometres) south-west of St. Pauls' Rocks. At Fernando de Noronha in 1954 (Hosoe, 1956) *Sagitta serratodentata atlantica* made up two-thirds of the chaetognaths, and was followed in order of abundance by *S. enflata, Pterosagitta draco, Krohnitta pacifica* and *Sagitta hexaptera.*

NOTES ON THE SEVERAL SPECIES

The reference under each species heading are to good descriptions which I have found useful in identification ; they are not lists of synonymies. The latter will be found in Ritter-Záhony, 1911 ; Michael, 1911, 1919 ; Johnston & Taylor, 1921 ; Burfield & Harvey, 1926 ; Burfield, 1930, 1950 ; Kramp, 1939 ; Tokioka, 1939, 1940*a*, 1940*b* ; Thomson, 1947 ; Pierce, 1951 ; Vannucci & Hosoe, 1952 ; David, 1955, 1956, 1958 ; Furnestin, 1957.

Whenever a species has been sufficiently numerous, I have shown the details of head armature etc. separately for young forms (stages O and I) and adults (stages II and up). This seems to me to be preferable to the more usual method of showing the range of variation within different size-groups (see, for example, Thomson, 1947), since the development of head armature is more a function of maturity than of size. Furthermore, I have shown, in addition to the range of variation, the numerical distribution within the range ; this method can show up specific and racial differences better than can the range of variation alone. At the end of the paper I have summarized the head armatures and tail lengths of the adults of the species in the *Rosaura* collection.

Sagitta friderici Ritter-Záhony

Ritter-Záhony, 1911 : 19.
Fraser, 1952 : 14.
Vannucci & Hosoe, 1952 : 14.
Faure, 1953 : 26.
Furnestin, 1954 ; 1957 : 113.

Mme. Furnestin (Faure, 1953 and Furnestin, 1954) has shown that *S. friderici* is distinguishable from *S. bipunctata*, but there has been some question as to whether *S. friderici* is separable from *S. tenuis* ; the latter point will be discussed in the section below on *S. tenuis*. Only two specimens of *S. friderici* occurred in the *Rosaura* collection, one from each of Stations 45 and 46. Both these were over deep water in the eastern central Atlantic, and bear out the suggestion of Vannucci & Hosoe (1952) that this species is not so neritic as was suggested by Faure (1953).

Length (mm.)	Tail (% length)	Hooks	Ant. teeth	Post. teeth	Stage
12·7	26	8	8	18	II
6·8	25	7	6	12	I

The best character by which this species can be separated from *S. bipunctata* seems to be the propinquity of the seminal vesicle to the posterior fin ; in *S. bipunctata* there is a gap, but in *S. friderici* there is not.

Sagitta tenuis Conant

Michael, 1911 : 72.
Pierce, 1951 : 219.
Tokioka, 1955 : 57.

This is not yet a well-known species, and several authors have cast doubt on its validity ; the only sound work on its distribution has been that of Pierce (1951, 1953, 1958) and of Bieri (1957).

Conant (1896) described *S. tenuis* rather inadequately from specimens taken in Kingston Harbour, Jamaica. Ritter-Záhony at first (1910*b*) regarded it as a synonym for *S. bipunctata*, but later (1911) listed it among a number of doubtful species. Michael (1911) re-examined Conant's material and kept *S. tenuis* separate from *S. bipunctata*. Pierce (1951) redescribed *S. tenuis*, but tentatively regarded it as a synonym for *S. friderici* on the grounds of its resemblance to Ritter-Záhony's (1911) description of the latter. Fraser (1952), however, in his valuable discussion of the confusion between *S. bipunctata* and other species, feels that *S. tenuis* should be kept separate from *S. friderici* if only because of the great difference in size between the two : *S. tenuis* less than 8 mm., mature *S. friderici* more than 10 mm. Tokioka (1955), after expression some preliminary doubt, comes to the conclusion that *S. tenuis* and *S. friderici* are both valid species, while Bieri (1957) suggests that, in the coastal waters of Peru and Lower California at any rate, the two species represent the ends of an unbroken sequence of ecotypic variation. Finally, Furnestin (1957) firmly separates the two, placing them both, together with *S. setosa* Müller, *S. hispida* Conant and *S. helenae* R.–Z., in her " groupe *friderici* " of neritic species.

After examining 103 specimens from Station 38A and 73 from Station 40 (both from tidal rivers in British Guiana) I am in no doubt that my material is identical with Pierce's *S. tenuis*, and that *S. tenuis* is a valid species separate from *S. friderici*.

From Station 38A there were 103 specimens, including 7 stage I, 48 stage II and 48 stage III ; in the 73 specimens from Station 40 there were no stage I, 22 stage II and 51 stage III. In the accompanying tables I have omitted those of stage I, because they had not yet acquired their full complement of teeth ; the two lots are shown separately because there are certain small differences between them, viz.

(1) *Front teeth :* most of those from Station 38A have 5, most of those from Station 40 have 6.

(2) *Anterior fins :* these begin somewhat further forward in station 38A than in Station 40, and are somewhat longer ; they end at about the same level in both lots.

In a separate table I also show the anatomical details of six *S. tenuis* kindly sent to me by Dr. Pierce, collected by him at Cedar Keys, Florida. As regards length, numbers of back teeth and front teeth, position of hind-end of anterior fins, and length of posterior fins, there is no difference between those from Florida and those from British Guiana. On the other hand the Floridan specimens have somewhat shorter tails (26–29% *v.* 27–33%), fewer hooks (7, 8 *v.* 8, 9), shorter anterior fins (16–21% *v.* 18–26%) which also begin further back (34–38% *v.* 29–36%), and less of the posterior fin on the tail (52–65% *v.* 58–75%). These differences do not seem more significant, however, than those already noticed between the two lots from British

Sagitta tenuis

Length			
mm.	38A	40	Total
>7	1	—	**1**
6·5–7	1	—	**1**
6–6·5	3	2	**5**
5·5–6	10	6	**16**
5–5·5	18	14	**32**
4·5–5	27	36	**63**
4–4·5	25	14	**39**
3·5–4	11	1	**12**

Tail			
% lgth.	38A	40	Total
<27	5	1	**6**
27	9	1	**10**
28	10	7	**17**
29	13	14	**27**
30	21	7	**28**
31	19	14	**33**
32	10	18	**28**
33	4	9	**13**
34	4	1	**5**
>34	1	1	**2**

	Hooks			Anterior teeth			Posterior teeth		
No.	38A	40	Total	38A	40	Total	38A	40	Total
3	—	—	—	—	—	—	—	—	—
4	—	—	—	10	—	**10**	—	—	—
5	—	—	—	69	13	**82**	—	—	—
6	—	—	—	14	40	**54**	2	—	**2**
7	1	—	**1**	—	17	**17**	3	—	**3**
8	55	44	**99**	—	1	**1**	6	1	**7**
9	38	28	**66**	—	—	—	6	3	**9**
10	—	—	—	—	—	—	14	10	**24**
11	—	—	—	—	—	—	18	12	**30**
12	—	—	—	—	—	—	20	20	**40**
13	—	—	—	—	—	—	13	12	**25**
14	—	—	—	—	—	—	17	7	**24**
15	—	—	—	—	—	—	1	6	**7**
16	—	—	—	—	—	—	4	1	**5**

Anterior fins

Anterior end			
% lgth.	38A	40	Total
28	4	—	**4**
29	8	1	**9**
30	10	2	**12**
31	11	6	**17**
32	23	16	**39**
33	18	15	**33**
34	6	17	**23**
35	6	9	**15**
36	2	5	**7**
37	1	2	**3**
38	2	—	**2**
39	2	—	**2**

Posterior end			
% lgth.	38A	40	Total
49	1	2	**3**
50	4	1	**5**
51	5	5	**10**
52	18	13	**31**
53	7	15	**22**
54	18	14	**32**
55	8	10	**18**
56	18	7	**25**
57	5	4	**9**
58	3	2	**5**
59	1	—	**1**
60	2	—	**2**
>60	3	—	**3**

Length of fin			
% lgth.	38A	40	Total
16	—	1	**1**
17	—	4	**4**
18	4	4	**8**
19	12	13	**25**
20	9	19	**28**
21	10	16	**26**
22	19	6	**25**
23	14	6	**20**
24	7	3	**10**
25	8	—	**8**
26	7	1	**8**
27	1	—	**1**
28	2	—	**2**

Gap between fins			
% lgth.	38A	40	Total
3	1	—	**1**
4	7	9	**16**
5	22	10	**32**
6	12	16	**28**
7	15	15	**30**
8	13	11	**24**
9	12	5	**17**
10	8	5	**13**
11	3	1	**4**
12	—	—	—
13	—	1	**1**

Posterior fins

Anterior end			
% lgth.	38A	40	Total
56	—	1	**1**
57	9	6	**15**
58	4	8	**12**
59	8	10	**18**
60	19	17	**36**
61	15	10	**25**
62	15	10	**25**
63	7	4	**11**
64	7	2	**9**
65	7	2	**9**
66	2	3	**5**
67	—	—	—
68	1	—	**1**
69	1	—	**1**

Posterior end			
% lgth.	38A	40	Total
84	2	1	**3**
85	5	3	**8**
86	7	13	**20**
87	19	21	**40**
88	32	23	**55**
89	12	9	**21**
90	13	2	**15**
91	3	1	**4**
92	1	—	**1**
93	1	—	**1**

Length of fin			
% lgth.	38A	40	Total
21	1	—	**1**
22	3	1	**4**
23	3	4	**7**
24	5	2	**7**
25	11	6	**17**
26	15	12	**27**
27	25	20	**45**
28	12	13	**25**
29	10	9	**19**
30	8	5	**13**
31	1	1	**2**
32	1	—	**1**

Percentage of fin on tail			
% lgth.	38A	40	Total
<58	5	2	**7**
58–59	4	3	**7**
60–61	5	2	**7**
62–63	12	8	**20**
64–65	12	11	**23**
66–67	20	14	**34**
68–69	13	15	**28**
70–71	12	8	**20**
72–73	3	3	**6**
74–75	3	3	**6**
76–77	2	2	**4**
>77	4	2	**6**

Six Sagitta tenuis *from Cedar Keys, Florida* (*Collected by Dr. Pierce,* 15.*iv*.49)

Length (mm.)	Tail (% lgth.)	Hooks No.	Ant. teeth No.	Post. teeth No.	Stage	Ant. fin. (% lgth.)	Ant. fin. (% lgth.)	Gap (% lgth.)	Post. fin. % lgth.)	Post. fin. (% lgth.)	Percentage of post. fin on tail
6·05	26	8	6	15	III	37–54	17	9	63–88	25	56
6·05	26	8	5	12	III	38–55	17	6	61–88	27	52
5·95	28	7	6	14	III	36–54	18	9	63–89	26	65
5·50	29	7	5	11	III	35–51	16	8	59–86	27	56
5·50	27	8	5	13	III	34–55	21	7	62–87	25	56
5·35	29	8	6	13	III	35–53	18	7	60–86	26	58

Guiana; in each instance there is an overlap, and there seem to be no grounds for regarding the Floridan and British Guianan specimens as belonging to different species. As mentioned above, Faure (1953) gives good reasons for keeping *S. tenuis* separate from *S. friderici*, but she also casts some doubt on the identity of Pierce's with Conant's *S. tenuis*. Pierce (1951), however, compared Conant's Jamaican syntypes directly with his own Floridan material and this, he states, " revealed that they were the same species ".

Hitherto not very much has been known about the distribution of *S. tenuis*. Pierce (1951) found it abundant on the west coast of Florida, where it flourished in a salinity of 35‰ but tended to avoid the most inshore waters where the salinity fell below about 25‰. (In the latter positions it was replaced by another small species *S. hispida* Conant.) Pierce (1953, 1958) also described its occurrence off North Carolina. Here *S. tenuis* is markedly neritic; its seaward distribution is limited by the 36‰ isohaline, and it is most abundant in such places as the southern mouth of the Pamlico Sound, where it occurs in salinities as low as, but not lower than, 22·7‰. The type locality of *S. tenuis* is Kingston Harbour, Jamaica, and other places mentioned by Pierce are various inlets and estuaries in the south-eastern United States where the salinity will be reduced, but not very reduced. Bieri (1957) records *S. tenuis* in the coastal current of Peru in salinities of 32–34‰ and temperatures of 18–20° C.

In the areas worked by Pierce and Bieri, then, *S. tenuis* seems to be confined to the salinity range 23–36‰. The *Rosaura* specimens show that in British Guiana it flourishes and breeds in salinities as low as 10‰. It would clearly be desirable to have a series of samples of *S. tenuis*, with salinity measurements, from various inlets and estuaries round the coast of Central America and from islands other than Jamaica.

Sagitta bipunctata Quoy & Gaimard

Ritter-Záhony, 1911 : 16.
Michael, 1911 : 41.
Ghirardelli, 1950 : 115.
Fraser, 1952 : 13.
Faure, 1953 : 36.
Furnestin, 1957 : 171.

S. bipunctata has often been confused with other species (see the valuable discussion on this point by Fraser (1952)), but Mme. Furnestin (Faure, 1953 ; Furnestin, 1954, 1957) has clearly established its identity and diagnostic limitations.

There were only six specimens in the *Rosaura* collection (it is too slender a species for the stramin net) ; one was from Station 13 off the eastern United States, and the others were all caught in the central Atlantic. Their specifications were as follows :

Length (mm.)	Tail (% length)	Hooks	Ant. teeth	Post. teeth	Stage
11·8	25	8	4	10	II
11·1	27	10	7	15	III
11·0	25	8	7	13	II
10·8	24	9	6	16	II
9·6	28	9	6	16	II
6·7	24	9	7	14	III

The smallest specimen had already reached stage III in maturity.

Sagitta elegans Verrill

Ritter-Záhony, 1911 : 14.
Fraser, 1952 : 7.
Fraser, 1957.

As mentioned earlier (p. 227) 43 young specimens were taken close to the Greenland coast. The largest was 9 mm. long, all were stage O juveniles, and none had acquired the adult number of teeth.

Sagitta robusta Doncaster

Ritter-Záhony, 1911 : 16.
Michael, 1919 : 259 (as *S. ferox*).
Burfield & Harvey, 1926 : 100.
Tokioka, 1939 : 127 (as *S. ai*).
Tokioka, 1940*a* : 4 (as *S. ai*).
Thomson, 1947 : 13.

" The identity of *S. robusta* is most confused " (Thomson, 1947). This statement is true if *S. ferox* Doncaster is regarded as a species separable from *S. robusta*, a point about which there has been much argument (see below) ; otherwise *S. robusta* is an easily recognized species, with its unusually large head and its stiff, slim body.

Doncaster (1902), when he described both species from the Indian Ocean, himself suggested that they might prove to be identical. Ritter-Záhony (1911) united them under the name *S. robusta*. Burfield & Harvey (1926), after re-examining Doncaster's original material, concluded that on balance it was better to regard *S. ferox* as a synonym of *S. robusta* ; they saw a large number of specimens.

On the other hand Fowler (1906), and after him Michael (1911), described a Far Eastern species as *S. ferox* and regarded it as separable, on the evidence of published descriptions, from *S. robusta* ; according to Thomson (1947), however, the *S. ferox* of Fowler and of Michael was really the *S. robusta* of Doncaster. Tokioka (1939 and 1940*a*), working in Japanese waters, found two species which he named *S. robusta* and *S. ai*, but according to Thomson Tokioka's *robusta* is really Doncaster's *ferox*, and *ai* is Doncaster's *robusta*. Finally Thomson says that in the waters south-east of Australia " the two are easily differentiated ".

The head armatures of *S. robusta* and *S. ferox* are almost identical, but Thomson (1947) gives the following characters on which to separate the two species (all figures expressed as percentages of total length) :

	Width	Width of head	Length of ant. fin	Length of Post. fin
S. robusta	6·1–6·6	9·4–11·4	25·5–30·4	25·4–30·8
S. ferox	5·4–5·8	7·7–8·3	21·1–22·7	25·0–27·0

Tokioka (1939) stresses another character, namely that the mature seminal vesical has a large head in his *S. robusta* (= *S. ferox* Doncaster) but not in his *S. ai* (= *S. robusta* Doncaster).

Unfortunately the 14 specimens of *S. robusta* from the *Rosaura* collection seem only to confuse the issue ; some of their characters are those of Thomson's *S. robusta*, but others of his *S. ferox*.

Width. After their long stay in alcohol the *Rosaura* specimens are bilaterally concave, and no longer suitable for width-measurement.

Length. They show no obvious signs of longitudinal contraction. The largest *Rosaura* specimen (stage II) measured 11·5 mm.; this suggests *S. ferox*. (Doncaster's *ferox* reached 13 mm., but his *robusta* 16 mm., while Thomson records a *robusta* as long as 22 mm.)

Width of head. This ranged from 9·5 to 12·2% of the body length, and 10 of the 14 specimens lay within the range 10·0–11·1%. This clearly suggests *robusta*.

Length of anterior fins. The anterior fins could be measured in 12 specimens, and ranged from 17·0 to 20·0% ; this as strongly suggests *ferox*.

Seminal vesicles. Only three specimens had vesicles which seemed to be mature, but none of them had a large head. As far as it goes this suggests *robusta*.

It should be noticed that each of these features in the *Rosaura* specimens belongs definitely to one or other of Thomson's species ; they are not intergrades between the two.

The other anatomical details of the *Rosaura* specimens are as follows :

Length (mm.)	Tail (% length)	Hooks	Ant. teeth	Post. teeth	Stage
11·5	25	8	10	12	II
11·2	26	7	10	12	II
10·9	26	7	8	12	II
10·6	26	7	9	12	II
10·4	24	7	8	12	I
10·4	27	8	9	12	I
10·0	26	7	8	15	II
9·6	26	7	8	11	II
9·5	26	7	7	12	I
9·1	24	8	8	13	I
8·6	28	8	9	13	I
8·4	27	7	7	12	I
8·3	27	7	7	12	I
5·8	28	9	7	11	O

Now, those who have found it difficult or impossible to separate *S. ferox* from *S. robusta* (Doncaster, Ritter-Záhony, Burfield & Harvey, Colman) have worked on material from either the Indian or the Atlantic Ocean. The Pacific Ocean, on the other hand, has provided the material for those (Fowler, Michael, Tokioka, Thomson) who have distinguished these two species. This discrepancy could, perhaps, be explained on the supposition that *S. robusta* is a single, though somewhat variable, species in the Indian and Atlantic Oceans, but is evolving in the Pacific Ocean into two recognizable subspecies, *S. robusta robusta* and *S. robusta ferox*. Such an explanation, if true, would be surprising, since the Indian Ocean is, in general, more closely linked faunistically with the Pacific than with the Atlantic.

Sagitta serratodentata Krohn

Ritter-Záhony, 1911 : 22.
Michael, 1911 : 39.
Thomson, 1947 : 15.
Ghirardelli, 1950 : 120.
Fraser, 1952 : 8.
Fraser, 1957.
Furnestin, 1957 : 147.

S. serratodentata was for long regarded as a single variable species. Tokioka (1940*b*) recognized two forms or subspecies *S. s. atlantica* and *S. s. pacifica* in Australian waters, and Thomson (1947) added a third form *S. s. tasmanica* from the same region. Fraser (1952) states that all three varieties occur together in Scottish waters, and doubts their subspecific validity ; but later (1957) he ascribes the variety *tasmanica*, in the eastern Atlantic, to more northern waters, and *atlantica* to warmer, southern and more saline waters. Furnestin (1957) firmly divides the species into three separate ones : *S. serratodentata* (= *f. atlantica*), *S. pacifica* and *S. tasmanica*.

The main character on which this separation is made is the structure and appearance of the mature seminal vesicle. There were 31 *Rosaura* specimens with mature seminal vesicles, and these were all of the *atlantica* type ; so fortunately, whatever the final decision on these taxa may be, the *Rosaura* material will still belong to *S. serratodentata*, the type-locality of which is Messina.

There were 95 *Rosaura* specimens, of which only five were caught by the stramin net (at Station 32 in the western Caribbean, and at 45 and 46 in the eastern central Atlantic) ; the other 90 all came from one short haul with the small silk net within a few yards of St. Paul's Rocks just before noon in bright sunshine. Table II (p. 226) shows that at the time of the *Rosaura*'s visit *S. serratodentata* was by far the commonest surface-living chaetognath at St. Paul's Rocks.

The smallest specimens measured 4·4 mm. (stage O), and the largest 9·6 mm. (stage III). The size-range and frequency of occurrence of the maturity stages were as follows :

Stage	Size-range (mm.)	Number
O	4·4–6·9	5
I	5·8–8·5	30
II	6·8–9·5	41
III	7·3–9·6	18
IV	7·85	1

Other details were as follows:

Sagitta serratodentata

Length				Tail (as % of length)				Hooks				Anterior teeth			Posterior teeth			
mm.	O, I	II–IV	Total	%	O, I	II–IV	Total	No.	O, I	II–IV	Total	O, I	II–IV	Total	No.	O, I	II–IV	Total
>9	—	13	**13**	*19*	1	—	**1**	*5*	—	—	—	2	—	**2**	*5–12*	5	—	**5**
8–9	5	34	**39**	*20*	2	—	**2**	*6*	4	28	**32**	2	—	**2**	*13*	7	—	**7**
7–8	17	12	**29**	*21*	—	—	—	*7*	27	30	**57**	8	1	**9**	*14*	3	2	**5**
6–7	8	1	**9**	*22*	4	7	**11**	*8*	4	2	**6**	11	17	**28**	*15*	7	8	**15**
5–6	3	—	**3**	*23*	3	11	**14**	*9*	—	—	—	10	33	**43**	*16*	10	10	**20**
4–5	2	—	**2**	*24*	11	18	**29**	*10*	—	—	—	2	8	**10**	*17*	1	8	**9**
				25	4	21	**25**	*11*	—	—	—	—	—	—	*18*	2	10	**12**
				26	9	3	**12**	*12*	—	—	—	—	1	**1**	*19*	—	6	**6**
				27	—	—	—								*20*	—	6	**6**
				28	—	—	—								*21*	—	2	**2**
				29	1	—	**1**								*22*	—	7	**7**
															25	—	1	**1**

Sagitta lyra Krohn

Ritter-Záhony, 1911: 8.
Ghirardelli, 1950: 109.
Fraser, 1952: 9.
David, 1955: 256.
Furnestin, 1957: 231.

Sagitta lyra, S. maxima and *S. gazellae* have, until recently, often been confused, in spite of the fact that Ritter-Záhony showed that the adults can be separated on tail-length alone:

Species	Tail (as % of length)
S. gazellae	10–14
S. lyra	14–18
S. maxima	19–25

There can be a certain amount of overlap between young *S. lyra* and old *S. maxima* and between young *S. gazellae* and old *S. lyra*, since in young stages the tail tends to be proportionately longer; almost all the adults, however, can apparently be sorted with confidence from Ritter-Záhony's figures.

Much of the confusion has been caused by the habit of these species of shedding some of their hooks and posterior teeth on reaching maturity; this habit is least marked in *S. maxima*, most marked as regards hooks in *S. lyra*, and as regards posterior teeth in *S. gazellae*. Formulae for head armatures are therefore of no value in these species unless the state of maturity is also given.

David (1955) has shown that *S. gazellae* is distinct from *S. lyra*, not only anatomically, but also geographically. *S. gazellae* is confined to the Antarctic and to the sub-antarctic south of the subtropical convergence, whereas *S. lyra* occupies subtropical and tropical latitudes; the two species overlap very little, if at all.

S. maxima is the only one of these three species in arctic waters, where it is abundant, and it also extends into the tropics and (David, 1958) to the Antarctic. It occurred regularly with *S. lyra* in the *Rosaura* catches throughout the Caribbean and the central Atlantic.

Furnestin (1957) has summarized observations on *S. lyra* by herself, Ghirardelli (1950) and Hamon (1952) in the general region of the Mediterranean and the water off north-west Africa ; these waters can be classified as warm-temperate to subtropical. She finds an unbroken sequence from younger forms with 6–10 hooks and 4–12 posterior teeth, through numerous intermediates with 5–9 hooks and 8–16 posterior teeth, to adults with as few as 3 hooks and 2 posterior teeth ; only in the last stage are the ovaries well developed (= my stages III and IV). Mr. David (in a letter) says that in southern subtropical waters *S. lyra* behaves in much the same way, losing hooks and posterior teeth gradually with advancing maturity ; in particular he mentions having seen *S. lyra* with 4 and 5 hooks.

This is in contrast to the *Rosaura* material, in which there are either 3 hooks (one has only 2), or 6 or more ; in 110 specimens there is not one with either 4 or 5 hooks on either side. The difference between the two lots was so striking that at first (before seeing either Furnestin (1957) or David (1955)) I thought that there were two species, each of which identified itself as *S. lyra*. Eventually, however, it became apparent that almost all of form A (6 hooks or more) were in stage I or II, and almost all form B (3 hooks) were in stages III or IV, as shown in the tables below. (I have divided other species into stages O and I as against stages II–IV or V, but the facts about *S. lyra* are more clearly shown by dividing them into forms A and B as defined above.)

Two of the *Rosaura* specimens came from Station 13 off the eastern United States, but all the rest were from ten tropical stations.

Size-range and frequency of maturity stages. There were none of stage O, and I have included two intermediate stages, I–II and II–III. In I–II the testis was still visible as such but there were already free sperms in the tail ; there were two examples, one with 8 hooks and 10 posterior teeth, the other with 3 hooks and 3 posterior teeth. In stages II–III some of the eggs had increased in size as in an ovary of early stage III, but the sperms had not been evacuated from the tail. There were seven in stages II–III ; six had 3 hooks, but one had 3 hooks on one side and 6 on the other ; four had from 5 to 9 back teeth, one had 3, one 2, and one had 3 teeth and 6 empty sockets whose teeth must have been very recently lost. (Incidentally, it is the posterior hooks and the lateral teeth which are lost.)

Stage	Size-range (mm.)	Number
I	13·6–26·0	6
I–II	13·5, 15·8	2
II	15·3–26·4	31
II–III	17·9–23·3	7
III	15·0–27·5	56
IV	16·9–26·7	7

Anatomical details are given below (columns A, 6 or more hooks ; columns B, 3 or 2 hooks).

All but two in group B were riper than stage II, whereas none in group A was riper than stage II ; this shows that in the tropical Caribbean and central Atlantic the shedding of both hooks and posterior teeth takes place (in the great majority of cases) during the evacuation of sperm from the tail, i.e., while the individual is advancing from stage II to stage III. Furthermore, five individuals with only 3

Length			Tail (% length)			Hooks			Ant. teeth		Post. teeth		Maturity		
mm.	A	B	%	A	B	No.	A	B	A	B	A	B	Stage	A	B
>27	—	1	*13*	1	3	*1*	—	—	—	—	—	1	*I*	6	—
25–27	3	11	*14*	4	7	*2*	—	1	—	—	—	35	*I–II*	1	1
23–25	6	22	*15*	10	28	*3*	—	70½	—	—	—	31	*II*	30	1
21–23	8	18	*16*	10	23	*4*	—	—	1	—	—	—	*II–III*	—	7
19–21	8	7	*17*	7	8	*5*	—	—	2	1	—	1	*III*	—	56
17–19	6	5	*18*	1	2	*6*	6	½	3	11	1	1	*IV*	—	7
15–17	5	7	*19*	1	1	*7*	20	—	13	40	3	—			
<15	1	1	*20*	3	—	*8*	8	—	16	20	7	2			
						9	3	—	2	—	10	1			
						10	—	—	—	—	14	—			
						11	—	—	—	—	2	—			

hooks still had five or more posterior teeth, whereas none in group A had fewer than 6 ; this shows that the hooks tend to be shed slightly in advance of the posterior teeth. The change-over is very abrupt in these tropical specimens, and not gradual (see above) as in subtropical waters.

Apart from the length of the tail, the claw-like hooks of fully mature *S. lyra* (Ritter-Záhony, 1911, fig. 8 ; Ghirardelli, 1950, fig. 2b ; David, 1955, fig. 5c ; Furnestin, 1957, phot. 45 and 47, fig. 93) serve at once to distinguish this species from *S. maxima*. David (1955) and Fraser (1957) describe a further difference ; in *S. maxima* the lateral nerve runs below the posterior fin, whereas in *S. lyra* the nerve splits and passes on each side of the fin.

Sagitta maxima (Conant)

Ritter-Záhony, 1910 : 264 ; 1911 : 8.
Fraser, 1952 : 8.

S. maxima greatly resembles *S. lyra* in size, transparency and flaccidity, but the former's tail is relatively longer and, as mentioned above, *S. maxima* never develops the claw-shaped hooks so characteristic of mature *S. lyra*.

Of the 167 specimens, 85 came from Station 8 off Greenland ; the rest were distributed fairly evenly through the remaining samples.

S. maxima is one of the few species in the *Rosaura* collection to show signs of geographic variation, as can be seen from the tables below. As regards tail-length and number of anterior teeth there is agreement throughout the range covered, but in length, number of hooks and number of posterior teeth, the Greenland specimens are distinct from the tropical ones ; those from Station 13 off the eastern United States are intermediate, but incline more towards the Greenland forms. (Station 13 produced 7 stage O and 5 stage I, but unfortunately no adults.)

Length. The 42 adults (stages II–IV) from Station 8 ranged in size from 42 to 59 mm., whereas those from Stations 27–46 ranged from 16·2 to 34·6 mm., leaving a gap between the two series of 7·4 mm. Admittedly, those from Station 8 were well preserved, whereas the others were all more or less contracted, but even so I do not think that the latter could ever have been nearly so large as the former.

Among the younger specimens, all-stage I from Station 8 were larger than those from any other stations, most of them being as big as the adults. The O's and I's from Station 13, while smaller than those from Station 8, are larger than those from the tropics and provide a link between the two.

Hooks. The adults of Station 8 all possessed 6, 7 or 8 hooks, whereas those from the tropics had 3, 4 or 5, with only one 6 and one 7.

The younger specimens present a less clear picture, because of their greater range in hook-number and because their numbers are few.

Posterior teeth. The adults from Station 8 have more posterior teeth than do those from the tropics, the majority having 5–8 as compared with 3–5. Again the greater range in the young stages obscures the picture.

In the following tables, adults (II–IV) are shown in heavy type. Station 8, Station 13 and Stations 27–46 are shown separately.

Sagitta maxima

	Length					
	St. 8		St. 13		Sts. 27–46	
mm.	O, I	II–IV	O, I	II–IV	O, I	II–IV
56–60	—	**5**	—	—	—	—
52–56	2	**11**	—	—	—	—
48–52	7	**11**	—	—	—	—
44–48	12	**10**	—	—	—	—
40–44	8	**5**	—	—	—	—
36–40	1	—	—	—	—	—
32–36	2	—	—	—	—	**3**
28–32	1	—	3	—	—	**12**
24–28	5	—	6	—	—	**20**
20–24	1	—	3	—	2	**17**
16–20	2	—	—	—	3	**6**
12–16	1	—	—	—	5	—
8–12	1	—	—	—	2	—

	Tail (as % of length)					
	St. 8		St. 13		Sts. 27–46	
%	O, I	II–IV	O, I	II–IV	O, I	II–IV
16	1	—	—	—	—	**1**
17	—	—	—	—	2	**1**
18	—	—	—	—	2	—
19	—	**1**	—	—	—	**2**
20	2	**3**	—	—	—	**1**
21	3	**9**	1	—	2	**6**
22	7	**11**	—	—	—	**6**
23	8	**7**	1	—	2	**7**
24	13	**6**	5	—	—	**7**
25	3	**2**	2	—	—	**8**
26	1	**2**	1	—	—	**5**
27	2	**1**	1	—	2	**9**
28	2	—	1	—	—	**2**
29	—	—	—	—	—	**1**
30	—	—	—	—	1	**1**
31	1	—	—	—	1	—

	Hooks						Anterior teeth						Posterior teeth					
	St. 8		St. 13		Sts. 27–46		St. 8		St. 13		Sts. 27–46		St. 8		St. 13		Sts. 27–46	
No.	O, I	II–IV	O, I	II–IV	O, I	II–IV	O, I	II–IV	O, I	II–IV	O, I	II–IV	O, I	II–IV	O, I	II–IV	O, I	II–IV)
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	—	—	—	—	—	—	5	**5**	—	—	—	**6**	2	—	—	—	—	**4**
3	—	—	—	—	—	**8**	16	**12**	1	—	3	**41**	3	—	—	—	—	**21**
4	—	—	—	—	1	**33**	14	**22**	9	—	4	**11**	7	**2**	2	—	2	**23**
5	2	—	—	—	1	**15**	5	**3**	2	—	1	**3**	7	**9**	4	—	3	**10**
6	4	**8**	—	—	4	**1**	2	—	—	—	4	—	15	**18**	5	—	2	—
7	17	**24**	1	—	1	**1**	1	—	—	—	—	—	7	**7**	1	—	1	—
8	7	**10**	9	—	1	—	—	—	—	—	—	—	2	**5**	—	—	1	—
9	5	—	2	—	2	—	—	—	—	—	—	—	—	**1**	—	—	2	—
10	8	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	1	—

Sagitta hexaptera d'Orbigny

Fowler, 1906 : 11.
Ritter-Záhony, 1911 : 7.
Michael, 1911 : 30 ; 1919 : 245.
Burfield & Harvey, 1926 : 95.
Burfield, 1930 : 210.
Thomson, 1947 : 10.
Fraser, 1952 : 9.
Vanucci & Hosoe, 1952 : 15.
Furnestin, 1957 : 201.

This large, transparent species was not found in the samples from Stations 8 and 13, but occurred regularly throughout the Caribbean and the central Atlantic. The specimens were quite well preserved (except for the fins) and were not contracted. The bodily proportions and head armature were very consistent throughout, and showed no sign of division into geographical races. The anterior teeth, which are long, thin, and project forwards in a very characteristic manner, afford the best diagnostic feature (see Furnestin (1957), fig. 81).

Of the 299 specimens, the smallest measured 6·6 mm. (stage O); the largest, though only in stage I, measured 38·7 mm.

The size-range and frequency of occurrence of the maturity stages were as follows:

Sagitta hexaptera

Stage	Size-range (mm.)	Number
O	6·6–28·2	35
I	11·4–38·7	133
II	14·0–36·6	112
III	15·7–28·5	15
IV	18·2–34·1	4

Other anatomical details were as follows:

Length				Tail (% length)				Hooks				Anterior teeth			Posterior teeth		
mm.	O, I	II–IV	Total	%	O, I	II–IV	Total	No.	O, I	II–IV	Total	O, I	II–IV	Total	O, I	II–IV	Total
36–40	1	1	**2**	*15*	1	—	**1**	*0*	—	—	—	—	—	—	—	5	**5**
32–36	1	7	**8**	*16*	—	2	**2**	*1*	—	—	—	—	—	—	5	32	**37**
28–32	13	4	**17**	*17*	5	3	**8**	*2*	—	—	—	13	16	**29**	49	60	**109**
24–28	19	28	**47**	*18*	7	7	**14**	*3*	—	—	—	107	87	**194**	41	20	**61**
20–24	38	57	**95**	*19*	9	16	**25**	*4*	—	—	—	44	28	**72**	27	10	**37**
16–20	48	32	**80**	*20*	31	46	**77**	*5*	1	4	**5**	3	—	**3**	36	3	**39**
12–16	36	2	**38**	*21*	33	25	**58**	*6*	2	10	**12**	—	—	—	8	1	**9**
8–12	9	—	**9**	*22*	37	18	**55**	*7*	67	44	**111**						
<8	3	—	**3**	*23*	21	8	**29**	*8*	32	53	**85**						
				24	12	4	**16**	*9*	41	17	**58**						
				25	10	1	**11**	*10*	23	3	**26**						
				26	1	—	**1**	*11*	2	—	**2**						
				27	1	—	**1**										

The *Rosaura S. hexaptera* were of additional interest in that some of them contained two-tailed cercarias which varied in body-length from 0·35 mm. to 1·2 mm. Out of 299 *S. hexaptera* 13 contained cercarias; one was in the gut, but all the others were lying free in the body cavity. They came from Stations 15, 27, 32 and 33, all in the Caribbean Sea. Dr. Dawes has been kind enough to examine them, and has identified them (Dawes, 1958) as *Cercaria owreae* Hutton (1954). No similar parasites were seen in any other species, though some (e.g. *S. enflata* and *S. maxima*) were quite as transparent as *S. hexaptera*, in which the cercarias were conspicuous.

In the sample from Station 45, one *S. hexaptera* contained many small multinucleate parasites in the body cavity, which Dr. Dawes thinks are not helminths.

Sagitta decipiens Fowler

Ritter-Záhony, 1911: 27.
Michael, 1919: 254.
Thomson, 1947: 20.

The 29 specimens of this somewhat slender species came from seven stations in the Caribbean and central Atlantic. Twenty-one were from two stations, 27 and 28, in the Gulf of Honduras; this may indicate that this species is commoner at the western extremities of the Caribbean Sea than it is elsewhere.

The specimens ranged in size from 6·3 to 13·5 mm. (both were at stage II). The size-range and frequency of occurrence of the maturity stages were as follows:

Stage	Size-range (mm.)	Number
O	7·6	1
I	8·8–11·1	6
II	6·3–13·5	22
III	—	0
IV	10·8	1

Other specifications were as follows:

Length (mm.)		Tail (% length)		Hooks		Ant. teeth		Post. teeth	
mm.	Total	%.	Total	No.	Total	No.	Total	No.	Total
12–14	**8**	*20*	**2**	*6*	**18**	*4*	**1**	*10*	**1**
10–12	**17**	*21*	**10**	*7*	**11**	*5*	**0**	—	—
8–10	**2**	*22*	**7**			*6*	**13**	*13*	**3**
6–8	**2**	*23*	**5**			*7*	**9**	*14*	**4**
		24–29	**5**			*8*	**6**	*15*	**6**
								16	**12**
								17	**1**
								20	**2**

Sagitta enflata Grassi David, 1956

Fowler, 1906 : 8.
Ritter-Záhony, 1911 : 13.
Michael, 1911 : 28; 1919 : 242.
Burfield & Harvey, 1926 : 95.
Thomson, 1947 : 11.
Vannucci & Hosoe, 1952 : 10.
Furnestin, 1957 : 213.

This medium-sized, transparent species occurred throughout the Caribbean and the central Atlantic, and also in Station 13 off the eastern United States (it was not found in Station 8 off Greenland). A few very young ones (the largest measuring only 3·1 mm.) were caught by the small silk townet in the harbour at Belize, British Honduras (Station 23). This agrees with previous records that *S. enflata* is one of the few oceanic species that penetrate inshore waters; on the Queensland coast, for example, it is the commonest species in the neritic waters between the Great Barrier Reef and the mainland (Burfield, 1950).

In one character, the number of anterior teeth, there is a difference between those from the temperate Station 13 and those from the tropical stations. Of the 14 specimens from Station 13, six had 5 anterior teeth, seven had 6 and one had 8; in the Caribbean and central Atlantic the great majority had 8 or 9, with a considerable number of 7's and 10's.

Of the 135 *S. enflata*, the smallest (excluding the very young ones mentioned above from Station 23) measured 5·2 mm. (stage O), and the largest was 17·1 mm. (stage II). The size-range and frequency of the developmental stages were as follows :

Stage	Size-range (mm.)	Number
O	5·2–10·8	9
I	7·3–15·0	48
II	7·3–17·1	56
III	11·5–16·5	20
IV	8·1, 15·0	2

The great size-range of each stage can, in the case of *S. enflata*, be explained by the fact that individuals of this species may breed several times, and continue to grow all the time (see Furnestin, 1957, p. 226).

Other specifications, which agree with previous accounts, are as follows :

Sagitta enflata

Length				Tail (% length)					Hooks			Anterior teeth			Posteri		
mm.	O, I	II–IV	Total	%	O, I	II–IV	Total	No.	O, I	II–IV	Total	O, I	II–IV	Total	O, I	II–IV	Total
16–18	—	6	**6**	*13*	—	4	**4**	*5*	—	—	—	6	2	**8**	—	—	—
14–16	2	21	**23**	*14*	2	4	**6**	*6*	—	—	—	1	7	**8**	1	—	**1**
12–14	11	35	**46**	*15*	7	12	**19**	*7*	—	1	**1**	5	9	**14**	1	—	**1**
10–12	20	12	**32**	*16*	9	22	**31**	*8*	—	4	**4**	17	15	**32**	—	—	—
8–10	14	4	**18**	*17*	17	14	**31**	*9*	30	32	**62**	21	28	**49**	3	—	**3**
6–8	8	1	**9**	*18*	7	8	**15**	*10*	19	34	**53**	6	13	**19**	6	5	**11**
4–6	1	—	**1**	*19*	6	7	**13**	*11*	7	6	**13**	—	4	**4**	3	3	**6**
				20	4	2	**6**	*12*	—	2	**2**	—	1	**1**	8	11	**19**
				21	3	3	**6**	*13*	—	—	—				8	12	**20**
				22	—	3	**3**	*14*	—	—	—				15	18	**33**
				23	—	—	—	*15*	—	—	—				4	7	**11**
				24	1	—	**1**	*16*	—	—	—				6	9	**15**
								17	—	—	—				1	8	**9**
								18	—	—	—				—	5	**5**
								19	—	—	—				—	1	**1**

Sagitta zetesios Fowler and ***Sagitta planctonis*** Steinhaus

David, 1956.

These two species were for many years placed together as *S. planctonis*, but the definitive paper by David (1956) shows that they are separate, and that *S. zetesios* is much the commoner of the two. The best character for separating them is the number of posterior teeth in almost all specimens except juveniles ; *S. planctonis* has less than 14, *S. zetesios* has more than 14. Further, in a summary of previous records, David states that *S. planctonis* is epiplanktonic in warm water, whereas *S. zetesios* is mesoplanktonic in most deep oceans except the Antarctic. The *Rosaura* specimens fully confirm David in the matter of posterior teeth and as regards abundance and horizontal distribution (*S. zetesios* occurred in Stations 8 and 13 and in all but two of the offshore tropical stations, *S. planctonis* only in Stations 45 and 46 in the eastern central Atlantic). Because open nets were used, however, the *Rosaura* material does not provide evidence about vertical distribution.

David (1956) describes a third species from this group (*S. marri*) which is confined to the Antarctic, and it is perhaps worth calling attention to the remarkable parallelism in geographical distribution between this group of species and the group

S. maxima-lyra-gazellae. Each group contains one species which is almost cosmopolitan (*S. zetesios* and *S. maxima*), one confined to the Antarctic (*S. marri* and *S. gazellae*), and one confined to warmer waters (*S. planctonis* and *S. lyra.*)

S. zetesios. *Length* (see tables below). The 15 specimens of *S. zetesios* from Station 8 were well preserved and very large, ranging from 31 to 42·5 mm. (David (1956) says " *Length* up to 40 mm."). The tropical specimens were all contracted and the largest (stage II) was only 24·3 mm. long ; I doubt whether any of the tropical ones could have been more than about 30 mm. long when alive. Part of this discrepancy can be explained by the greater age and maturity of the Greenland specimens, but even so stage I in Station 8 reached a size of 33 mm. The few specimens from Station 13 were intermediate as regards length.

Tail length. Those from Station 8 show a very narrow range of variation, all but three having tails 22 or 23% of the body-length. The much greater variation from the warmer stations is probably due to independently different degrees of contraction of trunk and tail.

Hooks. Station 8 shows fewer hooks (6–9) than the others (8–11). This may be an indication of racial difference, but David (in a letter) suggests that it is more likely due to the greater immaturity of the tropical specimens ; it is difficult, however, on the latter supposition to explain away the several tropical stage II with 10 hooks, while no stage I from Station 8 had more than 9. The absence of stage O from Station 8 seems to be real. Had they been present they would have been in the same size-group as *Eukrohnia hamata,* of which I picked out 139 from Station 8.

Anterior teeth. Here I think that the difference between Station 8 and the others is due solely to the maturest specimens (of which there were none from the tropics) having shed several teeth in the manner of *S. maxima* and *S. lyra.*

Posterior teeth. There seems to be no significant difference between Station 8 and the others.

S. planctonis. *Length and maturity.* In length *S. planctonis* was very similar to the tropical *S. zetesios* and was about as contracted, but the largest specimens were much more mature. There was only one stage III *S. zetesios* in Stations 13–46, a rather small specimen of 18·3 mm.; the older ones were probably living below the depth fished by the nets. The epiplanktonic *S. planctonis,* on the other hand, provided six fully matured stage III, three each of stages I and II, and no stage O.

Tail length. This covers much the same range of variation as in the tropical *S. zetesios.*

Hooks. David (1956) says " *Hooks* up to 11, usually 8–11 ". The few *Rosaura* specimens have 6–9, mostly 7.

Anterior teeth. There are fewer anterior teeth (5–7, mostly 5) in *S. planctonis* than in the tropical *S. zetesios* (7–13, mostly 8–11).

Posterior teeth. With the exception of a single very small (6·2 mm.) *S. zetesios* with only 10 teeth, there is here an absolute distinction (confirming David, 1956) between the two species. In the *Rosaura* specimens *S. zetesios* have 12 posterior teeth or more, *S. planctonis* have 10 or less.

The size-range and frequency of occurrence of maturity stages of these two species were as follows :

	Sagitta zetesios						*S. planctonis*	
	Station 8		Station 13		Stations 27–46		Stations 45, 46	
Stage	Size-range (mm.)	No.	Size-range (mm.)	No.	Size-range (mm.)	No.	Size-range (mm.)	No.
O	—	0	22	1	8·9–17·0	5	—	0
I	31–33	7	—	—	6·2–20·5	33	9·7–18·4	3
II	32·5–38	6	24–28·5	4	9·2–24·3	25	17·2–17·7	3
III	40, 42·5	2	—	—	18·3	1	18·9–26·9	6

Other specifications were as follows (*S. zetesios* on the left, *S. planctonis* on the right) :

	Sagitta zetesios									*S. planctonis*		
	Station 8			Station 13			Stations 27–46			Stations 45, 46		
Length (mm.)	I	II, III	Total	O	II	Total	O, I	II, III	Total	I	II, III	Total
40–44	—	2	**2**	—	—	—	—	—	—	—	—	—
36–40	—	5	**5**	—	—	—	—	—	—	—	—	—
32–36	4	1	**5**	—	—	—	—	—	—	—	—	—
28–32	3	—	**3**	—	1	**1**	—	—	—	—	—	—
24–28	—	—	—	—	3	**3**	—	1	**1**	—	1	**1**
20–24	—	—	—	1	—	**1**	2	5	**7**	—	3	**3**
16–20	—	—	—	—	—	—	6	12	**18**	1	5	**6**
12–16	—	—	—	—	—	—	16	7	**23**	1	—	**1**
8–12	—	—	—	—	—	—	13	1	**14**	1	—	**1**
4–8	—	—	—	—	—	—	1	—	**1**			

Tail (as % of length)

	S. zetesios						*S. planctonis*		
	Station 8			Stations 13–46			Stations 45, 46		
%	I	II, III	Total	O, I	II, III	Total	I	II, III	Total
17	—	—	—	3	2	**5**	—	2	**2**
18	—	—	—	8	3	**11**	—	1	**1**
19	—	—	—	5	4	**9**	—	—	—
20	—	—	—	9	6	**15**	—	4	**4**
21	1	1	**2**	3	5	**8**	1	1	**2**
22	3	4	**7**	3	5	**8**	1	1	**2**
23	3	2	**5**	2	1	**3**	—	—	—
24	—	1	**1**	3	1	**4**	1	—	**1**
25	—	—	—	3	2	**5**			
26	—	—	—	—	1	**1**			

Hooks

	S. zetesios						*S. planctonis*		
	Station 8			Stations 13–46			Stations 45, 46		
No.	I	II, III	Total	O, I	II, III	Total	I	II, III	Total
6	—	1	**1**	—	—	—	—	1	**1**
7	—	3	**3**	—	—	—	—	7	**7**
8	3	3	**6**	—	4	**4**	—	1	**1**
9	4	1	**5**	15	17	**32**	3	—	**3**
10	—	—	—	22	9	**31**			
11	—	—	—	2	—	**2**			

Anterior teeth

	S. zetesios						*S. planctonis*		
	Station 8			Stations 13–46			Stations 45, 46		
No.	I	II, III	Total	O, I	II, III	Total	I	II, III	Total
4	—	1	**1**	—	—	—	—	—	—
5	—	1	**1**	—	—	—	—	7	**7**
6	—	1	**1**	—	—	—	2	1	**3**
7	1	1	**2**	2	—	**2**	1	1	**2**
8	—	3	**3**	11	5	**16**			
9	1	—	**1**	6	5	**11**			
10	3	—	**3**	15	8	**23**			
11	2	1	**3**	2	8	**10**			
12	—	—	—	2	1	**3**			
13	—	—	—	1	3	**4**			

Posterior teeth

	S. zetesios						*S. planctonis*		
	Station 8			Stations 13–46			Stations 45, 46		
No.	I	II, III	Total	O, I	II, III	Total	I	II, III	Total
5	—	—	—	—	—	—	—	1	**1**
6	—	—	—	—	—	—	—	3	**3**
7	—	—	—	—	—	—	—	—	—
8	—	—	—	—	—	—	1	4	**5**
9	—	—	—	—	—	—	1	1	**2**
10	—	—	—	1	—	**1**	1	—	**1**
11	—	—	—	—	—	—			
12	—	1	**1**	1	—	**1**			
13	—	3	**3**	2	—	**2**			
14	—	1	**1**	3	—	**3**			
15	—	—	—	2	1	**3**			
16	4	—	**4**	7	3	**10**			
17	—	1	**1**	3	3	**6**			
18	3	2	**5**	4	5	**9**			
19	—	—	—	4	9	**13**			
20	—	—	—	9	5	**14**			
21	—	—	—	2	2	**4**			
22	—	—	—	1	2	**3**			

Sagitta neglecta Aida

Fowler, 1906 : 15.
Ritter-Záhony, 1911 : 23.
Michael, 1911 : 46 ; 1919 : 258.
Thomson, 1947 : 17.

There were seven specimens from five tropical stations (15, 23, 27 and 28 in the Caribbean, 46 in the eastern Central Atlantic).

Length (mm.)	Tail (% length)	Hooks	Ant. teeth	Post. teeth	Stage
8·8	25	10	6	12	III
8·3	24	7	8	18	II
7·2	25	7	8	13	II
7·2	26	8	5	14	I
7·0	27	7	6	11	I
6·5	22	6	8	13	I
6·2	31	7	3	9	O

Sagitta pulchra Doncaster

Fowler, 1906 : 17.
Ritter-Záhony, 1911 : 21.
Michael, 1919 : 251.
Thomson, 1947 : 19.

There were only two specimens, both from Station 42 off north-east Brazil.

Length (mm.)	Tail (% length)	Hooks	Ant. teeth	Post. teeth	Stage
9·6	22	5	8	16	III
8·5	24	6	7	16	II

Sagitta macrocephala Fowler

Fowler, 1905 : 65.
Ritter-Záhony, 1911 : 30.
Fraser, 1952 : 10.

This species is very easy to recognize, even with the naked eye, by its red colour and its large head. It is a deep-water species, and provided 107 specimens. It occurred off Greenland (Station 8), off the eastern United States (Station 13), in the Tongue of the Ocean in the Bahamas (Station 14), in two of the deepest hauls in the Caribbean (Stations 28 and 33), and in two of the deepest hauls in the central Atlantic (Stations 42 and 46). It was not picked out from the deep haul between Cuba and Jamaica (Station 15) ; two other regularly occurring species, *S. maxima* and *S. zetesios*, were also missing from Station 15.

The 19 specimens from Station 8 were well preserved and ranged in size from 12·5 to 21 mm. Those from other stations were badly contracted, and did not exceed 12·8 mm. The size-range (for what it is worth) and the frequency of maturity stages were as follows :

Stage	Size-range (mm.)	Number
O	5·2–11·6	20
I	5·15–19·0	60
II	8·1–21·0	25
III	20·5	1

Other specifications are shown below; *S. macrocephala* is remarkable for the even spread of the numbers of both sets of teeth in the adults, and for the range of numbers.

Sagitta macrocephala

Length				Tail (% length)				Hooks				Anterior teeth			Posterior teeth			
mm.	O, I	II, III	Total	%	O, I	II, III	Total	No.	O, I	II, III	Total	O, I	II, III	Total	No.	O, I	II, III	Total
20–22	—	3	**3**	*26*	1	—	**1**	*1*	—	—	—	1	—	**1**	*16–18*	6	—	**6**
18–20	1	3	**4**	*27*	2	—	**2**	—	—	—	—	—	—	—	*19*	3	—	**3**
16–18	—	—	**0**	*28*	4	1	**5**	*4*	—	—	—	—	1	**1**	*20*	5	—	**5**
14–16	7	1	**8**	*29*	5	1	**6**	*5*	—	—	—	3	2	**5**	*21*	9	—	**9**
12–14	7	2	**9**	*30*	5	3	**8**	*6*	—	—	—	14	3	**17**	*22*	4	—	**4**
10–12	5	7	**12**	*31*	7	2	**9**	*7*	—	—	—	35	8	**43**	*23*	3	1	**4**
8–10	18	10	**28**	*32*	16	1	**17**	*8*	—	—	—	14	4	**18**	*24*	8	3	**11**
6–8	34	—	**34**	*33*	11	6	**17**	*9*	—	—	—	9	5	**14**	*25*	4	2	**6**
4–6	8	—	**8**	*34*	7	3	**10**	*10*	—	1	**1**	3	3	**6**	*26*	8	—	**8**
				35	8	2	**10**	*11*	16	4	**20**				*27*	7	2	**9**
				36	5	1	**6**	*12*	44	14	**58**				*28*	5	4	**9**
				37	5	1	**6**	*13*	20	7	**27**				*29*	8	4	**12**
				38	3	2	**5**								*30*	3	1	**4**
				39	1	1	**2**								*31*	2	1	**3**
				40	—	2	**2**								*32*	1	2	**3**
															33	1	2	**3**
															34	2	2	**4**
															35	—	1	**1**
															37	—	1	**1**

Pterosagitta draco (Krohn)

Ritter-Záhony, 1911: 33.
Michael, 1919: 264.
Ghirardelli, 1950: 121.
Furnestin, 1957: 246.

This small, easily recognized species was taken in small numbers at almost every station in the Caribbean and central Atlantic. According to Burfield & Harvey (1926) and Thomson (1947) it lives mainly near the surface; accordingly it would have beeen encountered by the *Rosaura*'s nets only during the last few minutes of each haul, and in any case it is too small to be caught reliably by a stramin net. These considerations indicate, I think, that *P. draco* must be common or abundant throughout the tropical waters sampled by the *Rosaura*.

Burfield & Harvey (1926) record *P. draco* as abundant in the Indian Ocean, Burfield (1930) as abundant in the central Atlantic, Tokioka (1939, 1940*a*) as common in the warmer waters off Japan, Thomson (1947) as common to the south-east of Australia, and Pierce (1953) as common off North Carolina. Nevertheless Furnestin (1957) states: " les auteurs s'accordent à signaler sa rareté, non seulement en Méditerranée mais aussi dans l'Atlantique et le Pacifique (exception faite pour THOMSON, qui la classe parmi les espèces ' sub-dominantes ' au sud-est de l'Australie."

There are 45 specimens in the *Rosaura* collection, ranging in size from 4·4 mm. (stage II) to 7·8 mm. (stage III); many of them are rather contracted. The size-range and frequency of occurrence of the maturity stages are as follows:

Stage	Size-range (mm.)	Number
O	4·5, 4·7	2
I	4·85–6·25	8
II	4·4–7·45	14
III	5·5–7·8	18
IV	5·4, 6·5, 7·0	3

Other specifications are as follows :

Length		Tail (% length)		Hooks		Ant. teeth		Post. teeth	
mm.	Total	%	Total	No.	Total	No.	Total	No.	Total
7–8	**11**	*31–38*	**5**	*8*	**2**	*6*	**11**	*10–13*	**3**
6–7	**17**	*39*	**4**	*9*	**10**	*7*	**13**	*14*	**9**
5–6	**13**	*40*	**15**	*10*	**28**	*8*	**16**	*15*	**10**
4–5	**4**	*41*	**5**	*11*	**4**	*9*	**4**	*16*	**8**
		42	**5**	*12*	**1**			*17*	**6**
		43	**5**					*18*	**7**
		44	**3**					*19*	**1**
		45–47	**3**					*22*	**1**

Krohnitta subtilis (Grassi)

Michael, 1911 : 52.
Tokioka, 1939 : 135.
Thomson, 1947 : 22.
Vannucci & Hosoe, 1952 : 25.

The 11 specimens of this very slender species were all from tropical stations. Several authors have attempted to join *K. pacifica* with this species, but the descriptions of Tokioka (1939) and Thomson (1947), make it certain that the two species are distinct. Dr. Pierce kindly sent me a sample of his Floridan *K. pacifica*, which was a great help in confirming that all the *Rosaura* specimens do belong to *K. subtilis*. This is of some interest, in that both Tokioka in Japanese waters, and Pierce (1951, 1953) off Florida and North Carolina, stress the comparative scarcity of *K. subtilis* as compared with *K. pacifica.*

The details of the *Rosaura* specimens were as follows (there is only one row of teeth in *Krohnitta*) :

Length (mm.)	Tail (% length)	Hooks	Teeth	Stage
11·8	36	8	11	II
11·3	33	8	11	II
10·7	34	9	12	III
10·7	38	9	10	II
10·6	32	9	12	III
10·6	38	9	10	III
10·0	35	8	10	III
10·0	33	9	11	III
9·8	33	8	12	II
9·25	39	8	10	II
9·0	36	9	9	O

Eukrohnia hamata (Möbius)

Ritter-Záhony, 1910*a* : 268 ; 1911 : 39.
Michael, 1911 : 39.
Fraser, 1952 : 10.

As recently as 1947 Thomson stated that *E. fowleri* was synonymous with *E. hamata*, but there can be no doubt that, as most authors have maintained, the two species are separate. In *E. hamata* the eyes usually lack black pigment, the gut is not as a rule coloured red, and few, if any, have more than 11 hooks. In *E. fowleri* the eyes have a conspicuous patch of black pigment, the gut is a bright red, and few, if any, have fewer than 12 hooks. It seems probable that Thomson did not have any *E. fowleri* (a deep-living species) in his material.

As has been mentioned earlier, the *Rosaura* chaetognaths were sorted immediately after capture into red and colourless forms, and this served to separate 275 red *E. fowleri* from 204 *E. hamata* with only a single doubtful case. All the *E. hamata* had 7, 8, 9 or 10 hooks, whereas all but one of the *E. fowleri* had 12, 13 or 14 ; the exception was a very small (7·5 mm., stage O) *E. fowleri* with only 10 hooks, but this individual was too young to have developed its full complement of hooks and so does not affect the argument. *Not a single one of either species had* 11 *hooks on either side.*

There were 204 specimens of *E. hamata*, of which 139 were in the sample off Greenland (Station 8) agreeing with Kramp (1939) who found *E. hamata* abundant in these waters. It was again the most abundant chaetognath from Station 13 off the eastern United States, but after that there were only one between Cuba and Jamaica (Station 15), seven off NE. Brazil (Station 42) and six south-west of Dakar (Station 46), these last three being relatively deep tropical hauls. I found none in the Caribbean Sea. *E. hamata* has been recorded at the surface in both northern and southern high latitudes, but in low latitudes only at depths where the temperature stays below about 12° C. (Fowler, 1906 ; Ritter-Záhony, 1911 ; Johnston & Taylor, 1921 ; Burfield & Harvey, 1926 ; Burfield, 1930 ; Kramp, 1939 ; Thomson, 1947).

In *Eukrohnia*, in contrast to *Sagitta*, " spents " are not uncommon in which the ovaries remain visible as shrunken remnants ; following Kramp (1939) I have classified these " spents " as stage V.

As in the case of *Sagitta maxima* (q.v.) there seems to be some correlation between size and latitude. In Station 8 (off Greenland) the largest specimen measured 34 mm., in Station 13 (off the eastern United States) 25·2 mm., and in the tropical stations 16·1 mm. The tropical specimens were somewhat more contracted than the others, but never so much so as to make it possible that they were as large when alive.

The size-range and frequency of occurrence of the maturity stages were as follows :

	Station 8 (Arctic)		Station 13 (Temperate)		Stations 15, 42, 46 (Tropical)	
Stage	Size-range (mm.)	No.	Size-range (mm.)	No.	Size-range (mm.)	No.
O	9·5–19·5	21	11·2–23·0	12	—	—
I	16·5–27·5	25	10·7–24·5	25	7·2	1
II	20·0–31·0	52	18·7–24·2	9	9·4, 16·1	2
III	17·0–29·0	18	21·8–25·1	4	8·8–11·2	3
IV	20·5–34·0	18	—	—	9·5	1
V	20·5–29·0	5	25·2	1	13·3	1

Other specifications are shown below. (As with *Krohnitta*, *Eukrohnia* possesses only one row of teeth, but whereas those of *Krohnitta* appear to be homologous with the anterior teeth of *Sagitta*, those of *Eukrohnia* are clearly homologous with the posterior teeth of *Sagitta*.)

Eukrohnia hamata

Length			
mm.	O, I	II–V	Total
32–36	—	1	**1**
28–32	—	16	**16**
24–28	23	49	**72**
20–24	13	39	**52**
16–20	21	3	**24**
12–16	20	1	**21**
8–12	6	5	**11**
4–8	1	—	**1**

Tail (% of length)			
%	O, I	II–V	Total
20	1	—	**1**
21	4	3	**7**
22	7	7	**14**
23	7	10	**17**
24	7	14	**21**
25	8	6	**14**
26	11	13	**24**
27	6	14	**20**
28	9	18	**27**
29	7	18	**25**
30	5	3	**8**
31	6	4	**10**
32	3	1	**4**
33	2	2	**4**
34	1	—	**1**
35	—	1	**1**

Hooks			
No.	O, I	II–V	Total
7	—	1	**1**
8	19	17	**36**
9	58	87	**146**
10	7	9	**16**

Teeth			
No.	O, I	II–V	Total
3–9	14	1	**15**
10	3	1	**4**
11	4	1	**5**
12	5	—	**5**
13	2	1	**3**
14	1	—	**1**
15	4	1	**5**
16	—	3	**3**
17	1	5	**6**
18	9	18	**27**
19	13	18	**31**
20	12	15	**27**
21	3	15	**18**
22	7	17	**24**
23	1	12	**13**
24	2	3	**5**
25–28	3	3	**6**

Eukrohnia fowleri Ritter-Záhony

Ritter-Záhony, 1911 : 40.
Fraser, 1952 : 10.

The three main criteria for separating *E. fowleri* from *E. hamata* (colour, number of hooks, eye pigment) have been discussed above in the section on *E. hamata*.

Both species occurred together in several of the *Rosaura* hauls, but their relative abundance varied greatly. In the two most northerly stations (8 and 13) *E. fowleri* was much less abundant than *E. hamata*, but in the tropical stations it was much more so, and was, indeed, the commonest chaetognath in several of the samples. It was not found in every tropical haul, being absent from those where the estimated depth of the net was less than 900 m., and common only when the net went deeper than 1,000 m. *E. fowleri* is widely recognized as an inhabitant of considerable depths; in this respect it resembles the other red species, *Sagitta macrocephala*, whose incidence in the *Rosaura* collection was strikingly similar.

As in the case of *E. hamata*, *E. fowleri* reached a larger size in higher latitudes than in the tropics, but the difference was not so marked.

There were altogether 275 specimens of *E. fowleri*, of which all but 20 were caught in the tropics. The smallest was the 7·5 mm. juvenile with but 10 hooks already mentioned (p. 248) from the Gulf of Honduras (Station 28), and the largest measured 29·5 (stage I, Station 8).

The size-range and frequency of occurrence of the maturity stages were as follows :

Stage	Stations 8 and 13 (Arctic and Temperate) Size-range (mm.)	Tropical stations Size-range (mm.)	Total number
O	—	7·5–10·8	5
I	16·9–29·5	8·2–21·2	114
II	25·2–28·0	14·3–23·0	67
III	24·2–28·7	17·6–24·7	36
IV	—	18·0–21·6	5
V	27·0	17·6–27·8	38

Other specifications were as follows :

Eukrohnia fowleri

Length			
mm.	O, I	II–V	Total
28–32	2	3	**5**
24–28	2	16	**18**
20–24	6	60	**66**
16–20	36	62	**98**
12–16	51	5	**56**
8–12	19	—	**19**
4–8	3	—	**3**

Tail (% length)			
%	O, I	II–V	Total
17	2	5	**7**
18	9	6	**15**
19	12	12	**24**
20	22	14	**36**
21	31	26	**57**
22	16	31	**47**
23	9	21	**30**
24	10	9	**19**
25	4	12	**16**
26	2	4	**6**
27	1	2	**3**
28	1	3	**4**
29	—	1	**1**

Hooks			
No.	O, I	II–V	Total
10	1	—	**1**
11	—	—	—
12	52	49	**102**
13	64	89	**153**
14	1	9	**10**

Teeth			
No.	O, I	II–V	Total
10–15	24	—	**24**
16	3	—	**3**
17	10	3	**13**
18	7	2	**9**
19	12	4	**16**
20	8	1	**9**
21	6	2	**8**
22	16	11	**27**
23	10	16	**26**
24	10	18	**28**
25	6	23	**29**
26	4	24	**28**
27	3	20	**23**
28	—	11	**11**
29	—	5	**5**
30	—	5	**5**
31	—	—	—
32	—	2	**2**

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Summary of Tail-lengths and Head Armatures as Shown by the Great Majority of Adults (Stages II and up) in the Rosaura *Collection*

Species	Length (mm.)	Tail (as % length)	Hooks (No.)	Ant. teeth (No.)	Post. teeth (No.)
Sagitta friderici	12·7	26	8	8	18
S. tenuis	4–6	27–33	8, 9	4–7	10–14
S. bipunctata	6–12	24–28	8–10	6, 7	13–16
S. robusta	9–12	26	7	8–10	12
S. serratodentata	7–10	22–26	6, 7	8–10	15–22
S. lyra :					
Stages I, II	15–27	14–17	6–8	6–8	8–10
Stages III, IV			3		2, 3
S. maxima :					
Arctic	40–60	20–27	6–8	2–4	5–8
Tropics	16–35		3–5		2–5
S. hexaptera	16–36	18–23	6–9	2–4	1–4
S. decipiens	10–14	21–23	6, 7	6–8	13–16
S. enflata	7–17	13–20	9, 10	6–10	10–18
S. planctonis	16–25	17–22	7	5	6–8
S. zetesios :					
Arctic	32–44	21–24	7–9	4–11	12–18
Temperate and Tropics	10–28	17–25	8–10	8–13	15–22
S. neglecta	7–9	24, 25	7, 10	6, 8	12, 13, 18
S. pulchra	8–10	22, 24	5, 6	7, 8	16
S. macrocephala	8–22	30–40	11–13	5–10	24–34
Pterosagitta draco	4–8	39–44	9–11	6–9	14–18
Krohnitta subtilis	9–12	32–39	8, 9	10–12	—
Eukrohnia hamata	12–32	22–29	8–10	—	16–24
E. fowleri	12–32	17–26	12–14	—	22–30

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BY

J. E. HILL

Department of Zoology, British Museum (Natural History)

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By J. E. HILL

Only three specimens of this unusual Pygmy Squirrel, *Glyphotes simus*, have been recorded since publication of the description in 1898. It has received little attention in the literature, no doubt through the paucity of the available material, and has remained little known. The British Museum (Natural History) has recently received a specimen of *Glyphotes* from the Institute for Medical Research, Kuala Lumpur, and this accession has prompted further examination of the genus.

I am indebted to J. L. Harrison, lately of the Institute for Medical Research, who arranged the gift of *Glyphotes* ; to C. A. Gibson-Hill, Director, Raffles Museum, Singapore and to Tom Harrisson, Curator, Sarawak Museum, Kuching, who courteously loaned the material of *Glyphotes* in their care for comparison ; lastly, to R. W. Hayman, of the British Museum (Natural History), for his valuable advice and criticism during the preparation of this paper.

Apart from the original description, incidental mention in faunal works such as that of Banks (1931) and enumerations of the principal characters such as that of Ellerman (1940), previous published work on the genus appears limited to that of Chasen & Kloss (1927). Their paper gives a brief account of the known specimens at that date, with measurements, and records an additional specimen.

The following account is based on five specimens of *Glyphotes simus*, which so far as I have been able to ascertain represent the total preserved in collections at the present time. They are :

(i) British Museum 98.11.3.6. The type specimen. Adult, sex unknown. Collected on Mount Kina Balu, North Borneo, by A. Everett. Skin and skull, the rear of the cranium missing.

(ii) Sarawak Museum 55.11. Adult male. Collected on Mount Merapok (Mount Marabok), Brunei, by J. Waterstraat in December, 1899. Skin and skull, the latter not available : the Sarawak Museum collection was disorganized during the Japanese Occupation, 1941–45. Formerly British Museum 0.10.8.2 but given in exchange to the Sarawak Museum in 1901. As remarked by Chasen & Kloss (1927) the label has been marked " Co-type of the species ". However, as these authors point out, the specimen was collected in the year following publication of the description and no mention is made by Thomas of any specimen other than the type.

(iii) Sarawak Museum 55.12. Adult female. Collected on Mount Kina Balu, North Borneo at 3,500 ft. by a native collector on 10th September, 1913. Skin and skull: the latter not available (see (ii)). Formerly referred to *Callosciurus notatus*, which possibly explains why it was overlooked by Chasen & Kloss (1927).

(iv) Raffles Museum. Subadult female. Collected at Tenompok, Kota Bellud, near the south foot of Mount Kina Balu, North Borneo, by a native collector on 10th June, 1925. Skin and skull, the latter much broken and fragmentary.

(v) British Museum 58.446. Adult male. Collected at Tenompok, Mount Kina Balu, North Borneo, by a collector of the Institute for Medical Research, Kuala Lumpur, on 16th June, 1952. Specimen preserved in alcohol, the skull and baculum extracted and cleaned.

GLYPHOTES Thomas

1898 *Glyphotes* Thomas, *Ann. Mag. nat. Hist.* **2**: 250.

A genus of dwarf squirrel characterized by its short, broad rostrum, much reduced postorbital processes and peculiar, specialized incisors. The zygomatic plate slants upwards and is more nearly vertical than in *Callosciurus*. The lower jaw is weak, with low coronoid processes and slender, elongated condylar processes. The upper incisors are very broad and yet not thickened antero-posteriorly, their tips divergent from each other. The lower incisors are similar but are more strongly divergent. Cheek teeth 5/4, with their pattern as in *Callosciurus*.

Glyphotes simus Thomas

1898 *Glyphotes simus* Thomas, *Ann. Mag. nat. Hist.* **2**: 250. Mount Kina Balu, North Borneo.

Externally characterized by its deep, broad, short muzzle. A specimen in alcohol confirms the "stumpy-nosed" description applied by Thomas and indicates more than do study skins the depth of the muzzle in relation to its length. The ear is of the Callosciurine type and when laid forward reaches almost to the posterior canthus of the eye. The feet are of the normal tree squirrel pattern: of the four digits of the manus, D4 is slightly longer than D3 while the outer digits are equal in length and are about half the length of D4. The hallux is the shortest digit of the tarsus while D5 is considerably longer, nearly as long as D4, which only slightly exceeds in length D2 and D3. The claws are well developed, white tipped and dark brown at the base. The tail is rather narrow and is shorter than the head and body. External measurements (in millimetres) of B.M. 58.446: head and body 115, tail 95, hindfoot 27, ear 13.

The dorsum is dull grey, grizzled and flecked with pale buff. The dorsal pelage is typically of Callosciurine type, the short hairs of the underfur slate grey at the base and tipped with pale buff or straw colour. The longer, overlaying bristle hairs are black or chestnut based and are tipped with chestnut, with a subapical annulation of buff: not infrequently bristle hairs are found with dark tips and bases but with two annulations of buff separated by a central band of black. Occasionally, these hairs are black throughout their length. Essentially similar, but slightly shorter pelage extends over the nape and crown. The outer surfaces of the legs and the dorsal surfaces of the fore feet are the same colour as the back while the dorsal surfaces of the hind feet are slightly more buffy. The bases of the claws are furnished with a small tuft of brighter, more buffy hairs. The sides of the muzzle are brighter buff than the back and there is an orange buff eye ring. The ears, especially on their posterior edge, are fringed with bright orange buff. There is a very indistinct postauricular patch of white. The white lateral flank stripes are broad and are usually the same width throughout their length : in the type specimen they are broader anteriorly than posteriorly. The black sublateral stripes are narrower and less prominent, more diffuse, especially posteriorly, where a suffusion of black tends to spread across the belly. The anterior part of the ventrum is dull orange buff : posteriorly the ventrum is buffy but is suffused with grey and overlaid slightly with black. The tail is blackish, grizzled with bright orange buff. The hairs are dark tipped and dark based with a broad sub-basal annulation of bright buff, sometimes with a second subterminal annulation of paler buff separated from the sub-basal annulation by a band of black.

The specimen from Mount Merapok, Brunei, is brighter and less greyish dorsally than those from Kina Balu. Its tail hairs are annulated with brighter orange and the underparts are more buffy and less suffused with grey, while the dorsal surfaces of the feet are warmer in tone. This circumstance was noted by Chasen & Kloss (1927), who compared this specimen with that listed as (iv) above.

Externally, *Glyphotes simus* is similar to *Callosciurus notatus dulitensis*, from which it may be distinguished by smaller size, foreshortened muzzle, paler underparts and feet, broader, more prominent white lateral stripes, less prominent black sublateral stripes, greyer back and darker tail. Dorsally, it is similar in colour to *Callosciurus nigrovittatus orestes* but is paler and less buff. The annulations of the tail hairs are brighter than in *orestes* while the underparts are predominantly buff and not grey.

The baculum of *Glyphotes simus* (Plates 8 (*c*)–8 (*f*)) is of the Callosciurine pattern, as described by Thomas (1915) and figured by Didier (1952). It consists of two parts, a slender, tapering shaft and a separate plate or lamina attached to its dorsal surface.[1] The shaft, which at its base and for most of its length is greater in depth than in width, is comparatively broad based and tapers only slightly in its proximal half, but beyond its centre point tapers more abruptly to a blunt point furnished laterally with two small barbs. Viewed laterally, the ventral face forms a compound curve, the proximal half concave, the distal half convex. The dorsal surface is concave, more especially in its distal portion, whereon is attached the separate lamina. Viewed dorsally, the baculum is a slender, straight shaft. The lamina originates from a point just posterior to the tip of the shaft and extends along the dorsal surface for about half the length of the shaft. It is parallel-sided for most of its length but for its posterior quarter tapers to a point and is free from attachment to the shaft. Anteriorly, it is bluntly pointed. Measurements of the baculum (in millimetres) : length of shaft 13·2 and length of lamina, 6·6.

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[1] The surfaces of the baculum are described here according to the usage of Pocock (1923). The lamina is attached to that part of the shaft which in the extended penis is nearest to the belly, i.e. its upper or dorsal surface. The baculum, however, occurs in the distal portion of the penis which in the unextended condition is recurved to point posteriorly beneath the proximal portion of the penis. In this condition the lamina is ventrally placed in relation to the shaft.

It has been possible to examine the bacula of specimens representative of the following species of *Callosciurus*: *finlaysoni*, *erythraeus*, *flavimanus*, *notatus* and *prevosti*. Of these, the first three have the lamina attached to the central part of the shaft and not extending to the tip. The lamina is pointed anteriorly, is widest at a point some three-quarters of its length from the tip and tapers to a posterior point. The tip of the shaft is furnished with two lateral barbs and with a third, usually larger, dorsal barb. This structure is illustrated by Didier (1952). The bacula of *Callosciurus notatus* and *Callosciurus prevosti*, however, resemble that of *Glyphotes simus* in having the lamina, which is the same shape as in the preceding species, inserted immediately posterior to the tip of the shaft. Among other genera, the baculum of *Glyphotes* appears nearest to that of *Menetes*, but the lamina in this genus, although attached near the tip of the shaft, is very small and there are no discernible barbs.

The skull (Plates 7 (*a*), 7 (*b*), 8 (*a*)) is globular, with an exceptionally short, broad and deep rostrum. The junction of the nasals, premaxillae and maxillae forms an almost straight line joining the anterior edges of the anterior zygomatic roots. The nasals are short, broad and nearly parallel-sided, while the nasal aperture is flattened dorsally. The interorbital region is broad while the postorbital processes of the frontal are reduced and lie directly above the anterior edge of the posterior zygomatic root. The braincase is globular and not especially inflated. The orbit is more circular than in *Callosciurus* and is not placed especially far back, its anterior rim lying directly above p^4, with the lacrimal lying above p^4 and m^1. The zygomatic plate is weakly ridged and is slightly oblique, more vertical than in *Callosciurus*, its orbital edge ascending above the posterior face of p^4. The zygomatic arch is moderately strong with a small jugal process lying at the lowest part of the arch. The posterior zygomatic root is formed as in *Callosciurus*, the orbital surfaces of the alisphenoid and squamosal only slightly ridged and not forming a shelf as in *Nannosciurus*. The postorbital process of the jugal is rounded posteriorly as in *Callosciurus*. The anteorbital foramen is large, that part of the zygomatic plate lying over the infraorbital canal slightly reduced and narrow. The anterior palatine foramina are large and extend posteriorly to the maxillary suture. The palate is wide and terminates just beyond m^3, with no pronounced posterior palatal spicule. The maxillary tooth rows are parallel for much of their length but converge slightly posteriorly while the mesopterygoid fossa is moderate and the pterygoids not excessively developed. A narrow ectopterygoid is present. The bullae are not inflated. The mandible is weak with a minute coronoid process, lower in height than the condylar process, which itself is slender and much elongated posteriorly. The angular process is narrow and unthickened.

The incisors (Plate 8 (*b*)) are orthodont and very much specialized. The upper incisors are broadened but not thickened antero-posteriorly, their surfaces without grooves and with the anterior surface strongly convex. The outer lateral faces are strongly concave, the inner faces correspondingly convex so that for their terminal millimetre the teeth diverge from each other. The lower incisors are broadened, their anterior faces convex (not concave as stated by Thomas) and are not thickened antero-posteriorly. The lateral faces are similar to those of the upper incisors, the teeth similarly divergent at the tips. The lower incisors are worn into broad, flat chisel-shaped blades, the inner corners more worn than the outer, so that viewed from the front the teeth present a shallow V-shape. That these peculiarities are not artifacts caused during skull cleaning is proved by their presence in the spirit specimen examined. The cheek teeth are of normal Callosciurine pattern with p^3 not especially reduced and the upper molars not excessively ridged. In the mandible, p_4 is slightly smaller than the lower molars and m_3 is not elongated, while the antero-internal cusps of the lower teeth are high as in *Callosciurus*.

The following measurements (in millimetres) are those of an adult male (B.M. 58.446) with measurements of the type specimen in parentheses : the skull of the Raffles Museum specimen is too fragmentary for measurement, but some measurements obtained from this skull and of Sarawak Museum 55.11 appear in Chasen & Kloss (1927). Total length of skull 29·1 (—), condylobasal length 25·9 (—), occipitonasal length 28·9 (—), basal length 23·5 (—), zygomatic breadth 19·0 (—), braincase breadth 16·4 (16·5), nasals, length × breadth 6·6 × 5·2 (6·7 × 5·3), diastema 6·0 (5·7), palatal length 13·2 (12·5), height of muzzle behind incisors 6·3 (6·1), breadth of muzzle over roots of incisors 7·5 (7·8), bulla, length × breadth 5·5 × 3·3 (5·0 × 3·0), maxillary tooth row 4·8 (4·8), $i^1 - i^1$ (tips) 3·4 (3·2), length × breadth p^3 0·7 × 1·1 (0·6 × 0·7), length × breadth p^4 1·0 × 1·2 (0·9 × 1·3), length × breadth m^1 1·1 × 1·3 (1·1 × 1·3), length × breadth m^2 1·1 × 1·4 (1·2 × 1·4), length × breadth m^3 1·0 × 1·2 (1·0 × 1·2), orbital length 9·6 (9·5), length from lacrimal notch to tip of nasals 10·5 (9·6).

Apart from its specialized incisors and greatly shortened muzzle, the skull of *Glyphotes* is similar to that of *Callosciurus notatus*, although, of course, much smaller. Certain cranial characters, however, such as the slight backward deflection of the components of the orbit, the obliquity of the zygomatic plate, which although more nearly vertical than in *Callosciurus* is more oblique than in *Nannosciurus*, the reduction of the postorbital processes and their backward displacement, the slight backward displacement of the lacrimal, a more circular orbitotemporal fossa and the reduction of the coronoid processes tend towards *Nannosciurus*, *Prosciurillus*, *Sciurillus* and *Myosciurus*. The structure of the baculum, the dentition and the major cranial characters, however, associate *Glyphotes* indubitably with *Callosciurus*.

The genus *Glyphotes* was placed by Ellerman (1940) in his " Lariscus " section of Sciuridae, a heterogeneous group containing *Lariscus*, *Menetes*, *Rheithrosciurus*, *Rhinosciurus* and *Hyosciurus* (an assemblage which Ellerman admits is not a natural group) the principal criterion being that these genera are much specialized and distinct from *Sciurus*. Simpson (1945), following Pocock (1923), places *Glyphotes* in the Callosciurini or Oriental tree squirrels. The cranial, dental and more especially the bacular characters of *Glyphotes* however, associate the genus more closely with *Callosciurus* than was thought by Ellerman and it seems best regarded as an offshoot of the ancestral stem of this widespread Oriental genus. The remarkable resemblance in colour pattern to *Callosciurus notatus* appears to be the result of parallelism : this pattern, with slight variation, reappears in *Callosciurus nigrovittatus*.

Widely divergent views exist on the classification of the dwarf Sciuridae of Borneo, Celebes, West Africa and South America. Earlier authors, i.e. Forsyth Major (1893), Thomas (1914, 1914*a*) and Miller & Gidley (1918) unite the dwarf squirrels in a subfamily, Nannosciurinae, based on certain dental and cranial characters common to each. A less extreme view is taken by Ellerman (1940) who places *Nannosciurus*, *Sciurillus* and *Myosciurus* in a *Nannosciurus* section of Sciuridae. By inference, the genus *Prosciurillus*, erected by Ellerman (1947) for *Sciurus murinus* Müller & Schlegel, would be placed in this section by Ellerman. Others, i.e. Pocock (1923) deny any close relation, mainly from the study of the penial characters, and suggest that similarities between these genera are the result of convergence, a view apparently adopted by Simpson (1945), who places *Nannosciurus* (and by inference *Prosciurillus*), *Sciurillus* and *Myosciurus* with the Callosciurini, Sciurini and Funambulini respectively. An important but limited contribution is made by Anthony & Tate (1935), who compare *Nannosciurus*, *Sciurillus* and *Sciurus* and conclude that a close relation must be presumed to exist between *Sciurillus* and *Nannosciurus*, despite differences in their bacula.

The skulls and bacula of *Callosciurus*, *Glyphotes*, *Microsciurus*, *Prosciurillus*, *Sciurillus*, *Myosciurus* and *Nannosciurus* have been compared, examining particularly those characters shared by the four latter, more extreme genera. Dental characters have not been taken into account: all but the last two genera have molars with the normal Sciurine ridge and depression pattern. Although suppressed in *Myosciurus* and *Nannosciurus*, as pointed out by Ellerman (1940) it is occasionally possible even so to trace the pattern in some skulls. Suppression of the pattern is much less evident in *Prosciurillus* and *Sciurillus*. Attention has been directed towards characters likely to be modified by the small size and specializations (when compared with *Callosciurus* or *Sciurus*) of the dwarf genera. The results are presented in Table I, itself extended and adapted from the tabular comparison of Anthony & Tate (1935).

Moore (1958) has extended *Prosciurillus* as defined by Ellerman (1947) to include *Callosciurus leucomus*, a species with a shortened orbit and which Ellerman (1940) points out is "almost transitional" to the *Nannosciurus-Sciurillus* type of skull. There is much to commend this action: *leucomus* differs considerably from *Callosciurus*, *sensu stricto*, in the form of its orbit, in the posterior displacement of its postorbital processes and in the obliquity of its zygomatic plate. Ellerman (1949), while including *leucomus* within *Callosciurus*, in fact suggested that it might warrant subgeneric rank within that genus. Moore, however, does not indicate that at the same time *leucomus* differs somewhat from *murinus*, the type species of *Prosciurillus*. It has well developed postorbital processes (like those of *Callosciurus*) which are not displaced posteriorly as far as those of *murinus*: its orbit, while less elongate than that of *Callosciurus* is less circular than that of *murinus*: good series of skulls of both forms show that the lacrimal is less extruded into the margin of the orbit than in *murinus*: the coronoid process is less reduced: the articulatory area of the jugal and squamosal is not reduced: the zygomatic plate is more oblique than in *murinus* and the posterior edge of the nasals is less advanced from a line joining the anterior zygomatic roots. It is clearly transitional between *Callosciurus* *and* Nannosciurus

		Callosciurus notatus	*Glyphotes simus*	*Microsciurus similis*	*Microsciurus alfari*	*Prosciurillus leucomus*	*Prosciurillus murinus*	*Sciurillus pusillus*	*Myosciurus minutus*	*Nannosciurus melanotis*
1	Interorbital breadth / Length of frontal	0·82	0·93	0·79	0·81	0·85	0·81	1·00	0·96	0·87
2	Ectopterygoids	Slightly developed	Slightly developed	Very slight ridge	Very slight ridge	Well developed	Well developed	Well developed	None	Well developed.
3	Form of the orbitotemporal fossa	Elongate-oval	Less elongate, more circular	Similar to *G. simus* but more elongate	As in *G. simus* but more circular	Less elongate, more circular than *G. simus*	Almost circular, only slightly elongate	Circular	Circular	Circular.
4	Posterior displacement of postorbital process	None: lies above posterior face of m³	Slight: lies above anterior face of the posterior zygomatic root	Slightly more posterior than in *G. simus*	As in *M. similis*	Slight: much as in *G. simus* but slightly more posterior	More posterior than in *G. simus:* lies above centre of posterior zygomatic root	As in *P. murinus*	Displaced to rear of orbit: above rear of posterior zygomatic root	As in *M. minutus*.
5	Postorbital process	Well developed	Much reduced	Reduced	Reduced	Well developed	Reduced	Much reduced	Minute	Minute.
6	Posterior edge of suborbit	Posterior to postorbital process	Just posterior to postorbital process	As in *G. simus*	Directly below base of postorbital process	Just posterior to or beneath tip of postorbital process	Anterior to postorbital process	As in *P. murinus*	As in *P. murinus*	As in *P. murinus*.
7	Position of suborbit	Posterior to orbit	Extends to orbit	,,	As in *G. simus*	As in *G. simus*	As in *G. simus*	As in *G. simus*	As in *G. simus*	As in *G. simus*
8	Separation of frontal process of premaxilla from lacrimal by the maxillary-frontal suture	Moderate	As in *C. notatus*	As in *C. notatus*	As in *C. notatus*	More widely separated than in *C. notatus*	As in *P. leucomus*	As in *P. leucomus*	Wide separation	Wide separation.
9	Position of lacrimal	Mainly withdrawn from orbit: between frontal and zygomatic process of maxilla	As in *C. notatus*, but slightly extruded into orbital margin	,,	,,	As in *C. notatus*	Slightly extruded into orbital margin	More extruded	Extruded into orbital margin	Almost wholly extruded into orbital margin.
10	Upper incisors	Slightly proodont	Orthodont	Slightly proodont	Proodont	Proodont	Proodont	Strongly proodont	Strongly proodont	Strongly proodont.
11	Area of maxilla representing infraorbital part of masseter	Considerably less than area of region of premaxilla just anterior	As in *C. notatus*	Less than premaxillary area	As in *M. similis*	As in *M. similis*	About equal to premaxillary area	Slightly greater than premaxillary area	As in *C. notatus*	Greater than premaxillary area.
12	Presence of flange or ridge on orbital surface of alisphenoid from base of squamosal to origin of external pterygoid muscle	None or only slight	Very slight ridge	Incipient	Incipient	Very slight ridge	Incipient	Pronounced ridge	Pronounced ridge	Pronounced ridge.
13	Inflation of alisphenoid just anterior to bulla	None	Incipient	,,	,,	Incipient	Slight	Inflated	Inflated	Inflated.
14	Coronoid process	Normal	Much reduced: minute	Much reduced: minute	Reduced	Slightly reduced	Much reduced	Much reduced: minute	Obsolescent	Obsolescent.
15	Condylar process	,,	Slender: very elongate, hooked	Normal: slightly hooked	Slightly elongate: hooked	Slightly elongate: hooked	Elongate: hooked	Slender: elongate, hooked	As in *S. pusillus*	As in *S. pusillus*.
16	Posterior edge of nasals	Lie on a line joining anterior edges of orbits	As in *C. notatus*	Slightly anterior to this line	As in *M. similis*	As in *M. similis*	In advance of this line	As in *P. murinus*	Well in advance of this line	As in *M. minutus*.
17	Posterior palatal spine	Present	Minute	Absent	Absent	Present	Absent	Minute	Absent	Minute.
18	Insertion of internal pterygoid muscle	Not deep	Deeper than in *C. notatus*	Moderate	Deep	As in *G. simus*	Deep	Deep	Shallower than *P. murinus*	As in *M. minutus*.
19	Postorbital process of jugal	Present, flattened	Present, well developed	Present, well developed	Present, well developed	Present, well developed	Present, well developed	Absent	Present well developed	Present, well developed.
20	Articulation of jugal with squamosal	Broad jugal with extensive articulatory area	As in *C. notatus*	As in *C. notatus*	As in *C. notatus*	As in *C. notatus*	Articulatory area slightly reducd	Jugal slender, extensive articulatory area	As in *S. pusillus*	Jugal broad, articulatory area reduced.
21	Obliquity of zygomatic plate	Sharply oblique	Less oblique than in *C. notatus*	Slightly less oblique than *C. notatus*	As in *G. simus*	As in *M. similis*	As in *G. simus*	Nearly vertical	Vertical	Vertical.
22	Baculum	Slender shaft with blade-like lamina	As in *C. notatus*	Not seen	Not seen	Not seen	Not seen	Straight shaft with upturned spatulate tip	Straight shaft with thickened base and tip	Hinged, hook shaped shaft with lamina.

and *Prosciurillus murinus* and since its differences from the latter species are mainly small differences of degree it seems best included in that genus as defined by Moore. Furthermore, *Prosciurillus abstrusus*, described as new by Moore (1958) seems from the description to be intermediate in some respects between *murinus* and *leucomus*. *Microsciurus* has been included in Table I since, like *Prosciurillus*, it is a transitional genus between the true dwarf squirrels and the larger *Callosciurus* and *Sciurus*. *Microsciurus similis*, transferred to *Sciurillus* by Ellerman (1949), is considerably less specialized than that genus and for the purposes of the present paper is retained within *Microsciurus*.

Gradual divergence from the normal condition exemplified by *Callosciurus notatus* appears in a number of characters. Some of the characters examined are at least in part the direct result of the shortening of the base of the skull and its arcuate deflection. Such characters are the circular form of the orbit, the rearward displacement of the postorbital process, the separation of the frontal process of the premaxilla from the lacrimal by a projection of the maxilla, the extrusion of the lacrimal into the orbital margin, the forward extension of the suborbit, a tendency for the incisors to become strongly proodont, a lessening of the obliquity of the zygomatic plate and alterations in the form of the nasals. Others appear related to this cause less for mechanical reasons but through alterations in muscle attachments i.e. the development of alisphenoid ridges, increases in the relative area of the maxillary insertion of the masseter and alterations in the articulatory parts of the mandible. Yet others appear adventitious, such as the presence or absence of a post-palatal spine, the form of the jugal process and the presence or absence and degree of development of the ectopterygoids.

Sciurillus, *Myosciurus* and *Nannosciurus* are seen to be the most extreme genera. Of these, *Myosciurus* and *Nannosciurus*, the smallest genera, are the most divergent. *Sciurillus* occupies a position intermediate between *Microsciurus*, *Prosciurillus* and the extreme genera. *Myosciurus* and *Sciurillus* are further specialized in the form of the zygomatic plate, which in *Myosciurus* is greatly reduced and in *Sciurillus* is grooved above the anteorbital foramen. This aperture in *Prosciurillus*, *Sciurillus* and *Nannosciurus* lies well in advance of the anterior end of the maxillary tooth row. *Prosciurillus* and *Microsciurus* are transitional between *Glyphotes* and the more extreme genera and display many of their characters in lesser degree. The skull of *Microsciurus* closely resembles that of *Prosciurillus*, both genera displaying the characters considered here at about the same level of development. This factor no doubt led Ellerman (1940) to associate *Prosciurillus murinus* with *Sciurillus* and later (1949) to transfer *Microsciurus similis* to *Sciurillus*. Both genera, however, are less specialized than *Sciurillus*: *Microsciurus similis* (transitional to *Sciurus*) in fact stands further from *Sciurillus pusillus* than does *Prosciurillus leucomus* (transitional to *Callosciurus*) to *Prosciurillus murinus*. *Glyphotes* connects *Prosciurillus* and *Callosciurus* in the development of its skull while *Microsciurus*, considerably more advanced in the development of the characters considered, provides a more remote link between *Sciurillus* and *Sciurus*. Such bacula as have been examined suggest no relation between the genera. That of *Glyphotes* is typically Callosciurine, while the baculum of *Sciurillus* is said by

Anthony & Tate (1935) to resemble that of *Sciurus* (*Sciurus niger*). The baculum of *Myosciurus*, which stands somewhat apart from other Sciurid bacula, resembles most closely in its small size and terminally thickened rod-like form the bacula of the African tree squirrels. The hook-shaped, laminated baculum of *Nannosciurus* is nearest to the " Tomeutes " type of Thomas (1915). No regular pattern is displayed by the adventitious characters. The form of the postorbital process of the jugal is variable, but its position on the arch of the zygoma appears related to the shortening of the orbit. It is on or near the lowest part of the arch in *Callosciurus*, *Glyphotes*, *Microsciurus* and *Prosciurillus*. In *Myosciurus* and *Nannosciurus* it is pushed forward to a position on the anterior ascending part of the arch, while *Sciurillus* displays an intermediate condition.

There appears to be no intermediate genus comparable with *Glyphotes* or *Microsciurus* among the African tree squirrels. Reduction of size and relative shortening of the rostrum, however, occur within the genus *Paraxerus*, of which the smaller members, on account of certain external and dental characters, are usually considered a subgenus, *Tamiscus*. The larger species of *Paraxerus* (the *cepapi*, *flavivittis* and *palliatus* groups of Ellerman (1940)) have skulls similar to *Callosciurus* in many respects and show no trace of the specializations of dwarf genera. Some of these characters appear among the members of the subgenus *Tamiscus*, all of which are smaller and have a relatively shorter rostrum. The orbitotemporal fossa is shortened and less elongated than in the larger species and the postorbital processes are displaced posteriorly to lie slightly in advance of (*boehmi*, *emini*, *vulcanorum*, *antoniae*) or above (*alexandri*) the anterior face of the posterior zygomatic root. There is a very slight ridge on the alisphenoid and the upper incisors are more proodont than in the larger species. The mandible, however, has remained unspecialized and there is no lessening of the obliquity of the zygomatic plate.

The grouping of the Celebean genus *Prosciurillus*, the South American genus *Sciurillus*, the West African genus *Myosciurus* and the Bornean genus *Nannosciurus* in one subfamily is unconvincing on zoogeographical grounds. All are highly specialized genera, widely divergent from *Sciurus* or *Callosciurus*, sharing in common a number of cranial characters which appear mostly to be related to the common factor of greatly reduced size. *Prosciurillus*, the largest, is a " giant " among these pygmy genera, and is the least divergent from *Callosciurus*. They diverge considerably among themselves. *Myosciurus* is particularly aberrant, and so far as comparison has been possible, their bacula have been found to differ widely, usually resembling in each case the bacula of the more normal tree squirrels of the region in which the dwarf is found. Study of the " semi-dwarf " *Glyphotes*, *Microsciurus* and *Prosciurillus* reveals that the characters appearing in extreme form among the most divergent genera are found in them in lesser degree and that these intermediate genera connect the " Nannosciurinae " to *Callosciurus* and *Sciurus*. The characters show difference in degree within the genus : *Prosciurillus murinus* ranks closely to the more extreme *Sciurillus* but the larger *Prosciurillus leucomus* displays considerable affinity with *Callosciurus* and, in the absence of the smaller species, would possibly warrant subgeneric rank within *Callosciurus*. The evidence therefore suggests that rather than forming a unit with biological reality, the dwarf squirrels of Celebes, Borneo, West Africa and South America have evolved independently. The grouping by Simpson (1945) of these squirrels with the tree squirrels of their respective regions appears a more accurate representation of their relationships than placing them in an artificial group which ignores the genera connecting them to the other members of the Sciuridae.

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PLATE 7

(*a*) *Glyphotes simus.* Dorsal aspect skull and ventral aspect mandible. × 3·5.
(*b*) *Glyphotes simus.* Ventral aspect skull and dorsal aspect mandible. × 3·5.

PLATE 8

(*a*) *Glyphotes simus.* Lateral aspect skull and mandible. × 2·5.
(*b*) *Glyphotes simus.* Frontal aspect incisor teeth. × 3.
(*c*) *Glyphotes simus.* Dorsal aspect baculum. × 5.
(*d*) *Glyphotes simus.* Lateral aspect baculum. × 5.
(*e*) *Glyphotes simus.* Dorsal aspect tip of baculum. × 12.
(*f*) *Glyphotes simus.* Lateral aspect tip of baculum. × 12.

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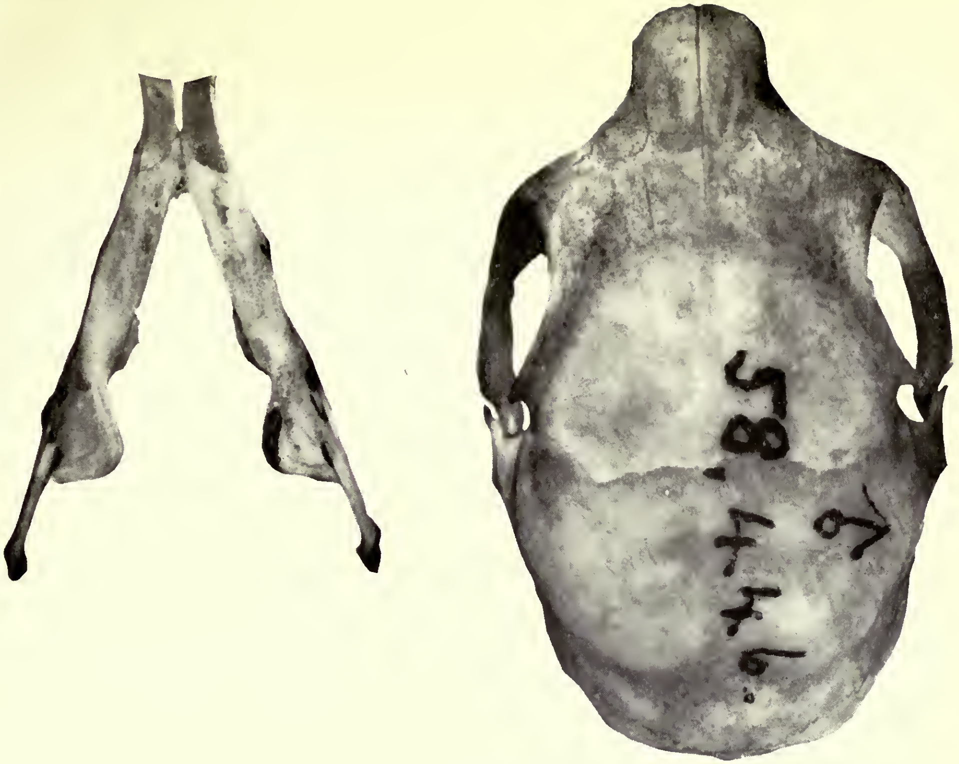


Plate 7(*a*).

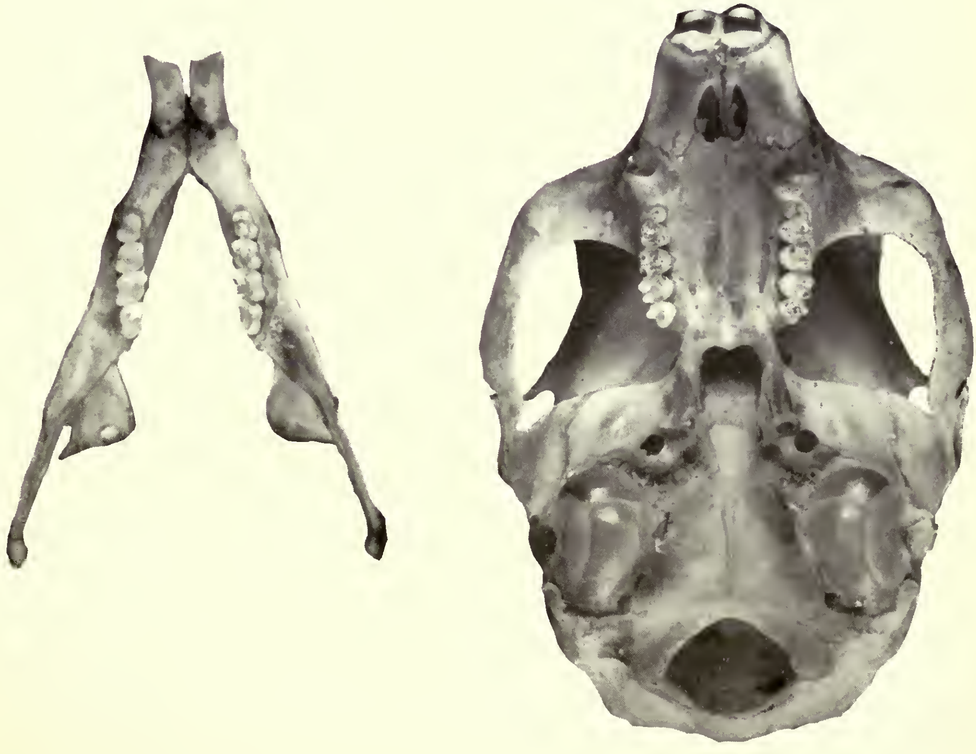
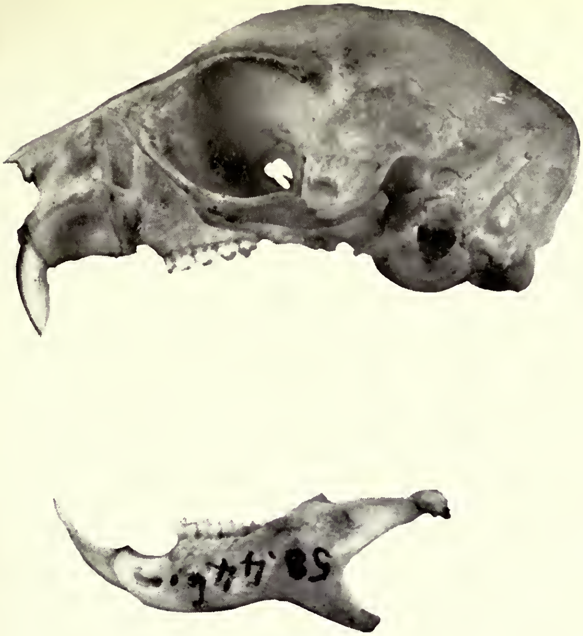


Plate 7(*b*).



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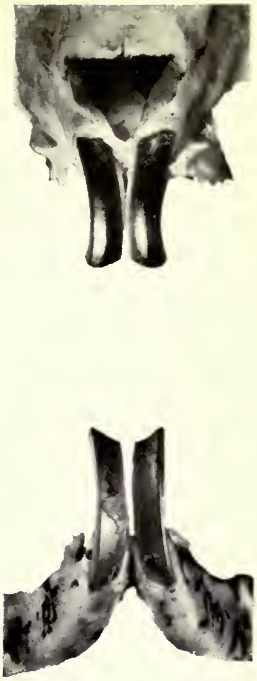

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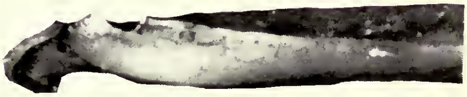

Plate 8(*e*).

Plate 8(*c*).

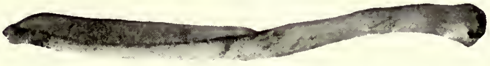

Plate 8(*d*).

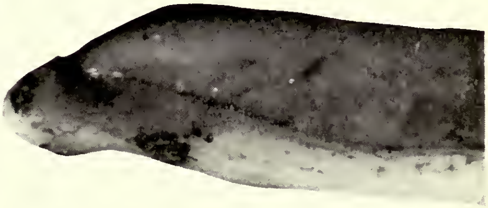

Plate 8(*f*).

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3.

REVISION OF THE WORLD SPECIES OF *APLYSIA*

(GASTROPODA, OPISTHOBRANCHIA)

N. B. EALES

BRITISH MUSEUM
2 - FEB 1960
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ZOOLOGY Vol. 5 No. 10
LONDON : 1960

REVISION OF THE WORLD SPECIES OF *APLYSIA* (GASTROPODA, OPISTHOBRANCHIA)

BY

N. B. EALES, D.Sc.

Zoology Department, University of Reading

BRITISH MUSEUM
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Pp. 267–404 ; *Frontispiece ;* 51 *Text-figures*

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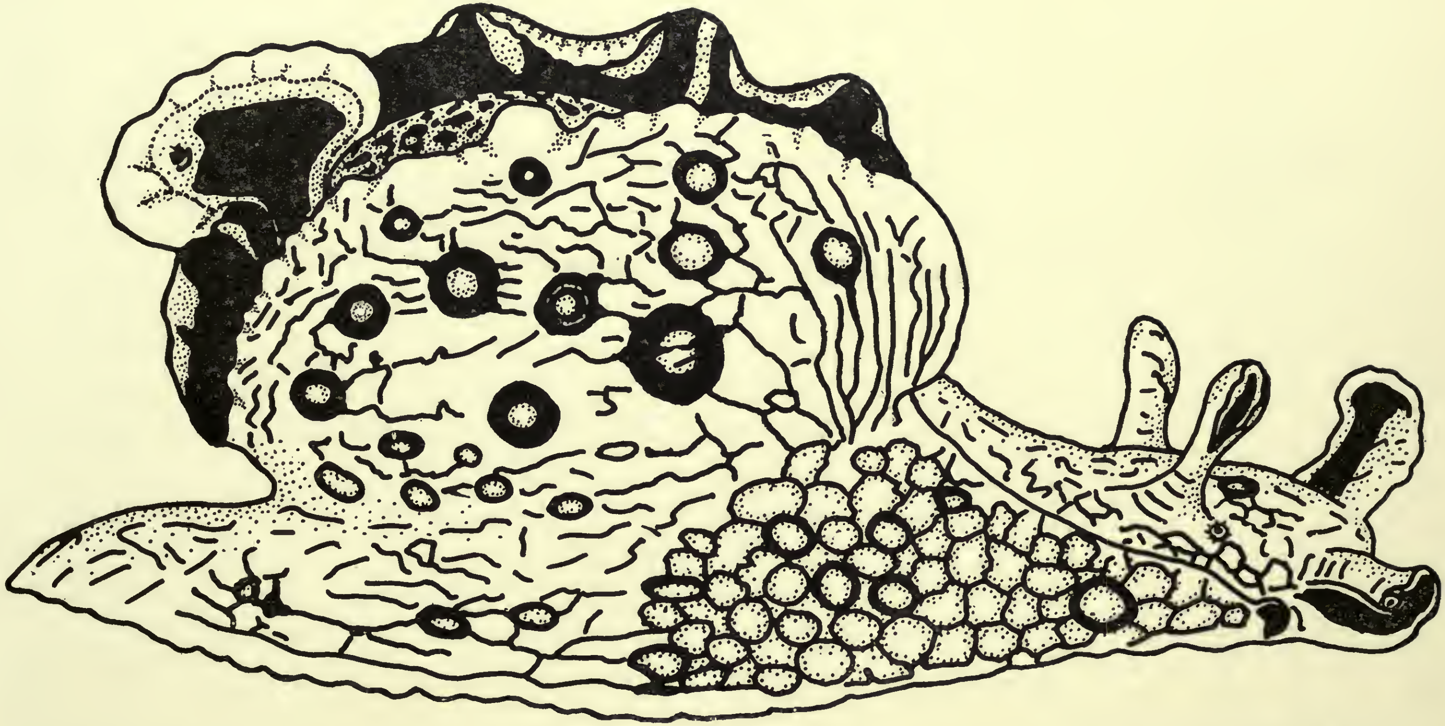

Aplysia dactylomela. From a painting of the living animal made in 1841 by Dr. J. Stuart and reproduced by Hutton, 1923, labelled *Tethys angasi* Sowerby. The rings on the skin are irregular in size and thickness, and are linked by fine reticulations; they have light centres. The edges of the parapodia are pale and fimbriated, inside they are barred with vertical black bands. Posteriorly the parapodia unite low down, level with the floor of the mantle cavity, fully exposing the large, broad, fluted anal siphon. $\times \frac{1}{2}$.

[*Frontispiece*]

REVISION OF THE WORLD SPECIES OF *APLYSIA* (GASTROPODA, OPISTHOBRANCHIA)

By N. B. EALES, D.Sc.

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SYNOPSIS

A review of the genus *Aplysia* and of the geographical distribution of its members has been made, based on the collections of the British Museum (Natural History) with comparative material from other national museums of Natural History, Marine Biological Stations and private collectors all over the world. The genus can be divided into five subgenera : *Pruvotaplysia*, the most primitive, with two species ; *Neaplysia*, North American, with probably only one species ; *Varria* nov., with more than twenty species ; *Aplysia*, with six species ; and *Phycophila*, of the Pacific, with one, possibly two species.

Full descriptions of the species are given, and the following new species are described : ***cronullae*, *dura*, *gracilis*, *rehderi*, *reticulata***, as well as a new variety, ***delli*** of *A. **nigra***. Their affinities with one another and with other subfamilies of the Aplysiidae are discussed.

1. INTRODUCTION

(a) *Definition of the Subfamily and Genus*

The Tectibranch family Aplysiidae contains four subfamilies :

Aplysiinae : *Syphonota* and *Aplysia*.
Dolabellinae : *Dolabella*.
Dolabriferinae : *Dolabrifera*, *Petalifera*, *Phyllaplysia*.
Notarchinae : *Notarchus*, *Stylocheilus*, *Barnardaclesia*, *Bursatella*.

The Aplysiinae are mostly large molluscs, with humped body, the skin usually with reticulate black markings, but without warts or villi. There are no separate oral lobes. The cephalic tentacles are broad and folded, the rhinophores slit like hare's ears. The foot has a short or moderately elongated tail. The parapodia are well developed, symmetrical, mobile, upstanding, separated anteriorly, free or joined posteriorly, typically natatory. The mantle encloses the shell, with or without a mantle foramen. Sub-pallial glands secrete either a purple or a white fluid. The anal siphon is usually tubular and erect, the opaline gland simple or compound. The genital aperture is inside the dorsal slit, anterior to the ctenidium. Shell narrow to broad, flexible, with reduced calcareous layer and apex, with an anal sinus on the right posterior border. Jaws large, radula with wide, denticulate rhachidian tooth and bi-serrate laterals. Caecum with a typhlosole present. Penis unarmed, penis sheath rarely armed, no penial collar. Nerve ring with three pairs of ganglia, pleurovisceral cords long, supra-intestinal and visceral ganglia adjacent, forming a pair or fused. There are two genera, *Syphonota* and *Aplysia*.

SYPHONOTA Adams, 1854[1]

Head broad, with rhinophores set close together and far back between the anterior ends of the parapodia. Foot broad. Parapodia free posteriorly, the backwardly directed anal siphon projecting through the gap between them, the shell and mantle tilted towards the animal's left side. Purple glands present. Opaline gland simple, multiporous. Genital aperture almost mid-dorsal, not covered by the mantle flap. Caecum not reaching the surface of the digestive gland.

Type species *Siphonotus geographica* Adams & Reeve, 1850. Circumtropical. Probably only one species. Baba (1955, pl. 1) gave a good coloured figure of this species.

APLYSIA L., 1767

Body soft in most species, elongated but strongly contractile, assuming the "sitting hare" position. The head is more shapely than in *Syphonota*, with erect rhinophores not far distant from the cephalic tentacles, so that a neck region is present between the head and the parapodial attachment. The foot varies from narrow to medium or broad, with a relatively short tail. The upstanding parapodia are mobile and usually natatory, joined high up in some species, shutting in the mantle cavity posteriorly ; meeting or joining low down on the foot in others, so that the mantle cavity, as in *Syphonota*, is open at both ends. Anal siphon erect. Secretion from the mantle glands purple except in the subgenus *Aplysia* where it is white or black. Opaline gland simple or compound, multiporous or uniporous respectively. Penis varying from short and broad to long and filiform, penis sheath smooth distally except in subgen. *Aplysia* where it is lined with warts bearing spines. Shell ovate or rounded, horny, with an imperfect calcareous lining ; in the subgenus *Neaplysia* the apex of the shell is flattened and rectangular, in all others recurved or hooked. Radula large, multiserial, all the teeth denticulate in most species except for a few vestigial teeth at the end of the row. Caecum appearing on the surface of the digestive gland. Cerebral ganglia distinct or fused. Parietal (supra-intestinal) and visceral ganglia free or fused.

---

[1] To replace *Siphonotus* Adams & Reeve, 1850 (*nec* Brandt, 1837).

Numerous species, most of which are tropical; others live in the temperate zone up to high latitudes.

Type species *A. depilans* Gmelin. European.

(b) *Subgenera*

The genus *Aplysia* can be divided into five subgenera:

1. *Pruvotaplysia* Engel, 1936, type *Aplysia parvula* Guilding in Mörch, 1863, a primitive subgenus with two species.

2. *Neaplysia* Cooper, 1863, type and only species *A.* (*N.*) *californica* Cooper.

3. *Varria*[1] nov., type *Aplysia dactylomela* Rang, 1828. Twenty-five species are here recognized.

4. *Aplysia* Linnaeus, 1767 (as *Laplysia*, probably a printer's error), type *A. depilans* Gmelin, 1791[2]. Six species, on one of which, *A. juliana* Quoy & Gaimard, was founded the subgenus *Tullia* by Mme. Pruvot-Fol, who did not realize that its peculiarities were shared by the type species of the genus.

5. *Phycophila* A. Adams, 1861, type *Placobranchus euchlora* M. E. Gray, 1850 (ex Adams unpublished). This subgenus includes oceanic floating Aplysias known in the Pacific Ocean and belonging to one or possibly two species.

Characters of the Subgenera

1. *Pruvotaplysia*. The foot is narrow, with a pointed tail; the parapodia are joined high up posteriorly, closing in the mantle cavity behind. There is a flat, unrayed mantle aperture over the strongly concave shell, which usually has remnants of a spiral at its apex. The mantle glands secrete purple, the opaline gland is simple and multiporous, the radula small, with not more than 40 rows and fewer than 25 laterals on each side in a row. The ganglia of the nerve ring and of the visceral group (supra-intestinal and infra-intestinal plus visceral) are rounded and distinct. All these features can be regarded as primitive. There are two species, *parvula* the type and *punctata*, the former circumtropical, the latter in the north temperate and arctic Atlantic areas of the Old World.

2. *Neaplysia*, with one species, *californica*. Giant forms, with strongly mottled skin. Foot broad, but with a long slender tail. Parapodia joined posteriorly low down. Mantle aperture minute or closed. Purple secretion from the mantle glands. Opaline gland large, compound, uniporous. The only peculiarity of this subgenus is the shell, which has a flattened calcareous apex, instead of a reduced spiral or hook. This rectangular flattening was described by Cooper (1863) as an accessory plate, but is part of the shell itself. In all other features the affinities are with subgenus *Varria*. The species is confined to the eastern North Pacific area.

3. *Varria*. This group contains about seven-tenths of the known species, which

---

[1] *Varria* from Varro, the name of a famous Roman scholar and writer.

[2] Opinion 200 of the International Commission on Zoological Nomenclature. See p. 396.

show remarkable generalization of structure, despite a great range of size. The parapodia are joined low down posteriorly, exposing the mantle cavity to a through current, since it is open at both ends, and although the anal spout is typically erect, it can be directed backwards between the parapodia as in *Syphonota*. In a few species, e.g. *inca*, *rehderi*, preserved specimens exhibit a low wall not more than 10 mm. high posteriorly, but in the living animal this probably forms a flat extension of the mantle floor, as it does in other species. It is quite unlike the high fusion in the subgenera *Pruvotaplysia* and *Aplysia*. There is always a purple secretion from the mantle glands. About half the members of this group have a simple multiporous opaline gland, the other half a compound uniporous gland, with gradations between them in some species, e.g. *cornigera*, *keraudreni*, *pulmonica*. The foot is narrow in the majority, of medium width in *cervina*, *oculifera* and *winneba*, and broad in *dactylomela*, *denisoni*, *gigantea*, *keraudreni* and *pulmonica*. The penis is filiform in *cronullae*, *fasciata*, *keraudreni*, *kurodai*, *sowerbyi*, *sydneyensis*, *willcoxi* and *winneba*, broad and spatulate in *dactylomela*, *denisoni*, *gigantea* and *pulmonica*, but tapering in the remaining species. The shell varies, but it never possesses a flat, plate-like apex, and is usually rather shallow. The radula is well developed, with many rows (up to about 80) and numerous laterals (to approximately 60) ; the laterals are multidenticulate except in *dactylomela* and *pulmonica*, where the denticulations exhibit feeble development in young teeth but disappear later, producing long, smooth-edged cusps, usually with a single stout lateral denticle. The caecum is straight or only slightly bent at the tip. The nerve ganglia exhibit fusion of the cerebral and of the visceral pair, except in *sagamiana*, which has small rounded discrete ganglia as in *Pruvotaplysia*. In its small size, simple multiporous opaline gland and narrow foot, *sagamiana* resembles *parvula*, but in its small rayed mantle aperture, rather flat shell without spiral apex and low junction of the parapodia posteriorly its affinities are with *Varria*. The distribution is in all oceans except the Arctic and Antarctic regions. Type *A. dactylomela*.

4. The subgenus *Aplysia* includes the type species of the genus, *A. depilans*. The body is low and flat, bulky, with a broad head. There is a broad foot, capable in most species of producing posteriorly a rounded but temporary sucker. The rather small parapodia are joined high up posteriorly. There is a flat mantle aperture. Purple is not secreted, but both the mantle glands and the simple, multiporous opaline gland secrete a white fluid, rarely a black, which is copious and odoriferous in the case of the opaline gland. The radular teeth are simple, but the number of rows and of teeth in a row reaches the maximum for the genus. The salivary glands are broad and flat, the caecum spiral at the tip. The penis is stout, heavily pigmented, and lies in a sheath which is armed with spiny warts. Six species are known. Distribution circumglobal in tropics and sub-tropics.

5. *Phycophila*. This includes small floating species, about which little is known. Only one species, *euchlora*, from the western Pacific area, has been described. The cephalic tentacles are broad, curved and pointed, the body slender, with a narrow foot and long, tapering tail. The parapodia are freely mobile and meet low down on the tail. The mantle is small, the shell sac closed. The opaline gland is small, simple and multiporous. The penis is filiform.

List of Recognized Species of Aplysia

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Rejected Names

Names considered invalid or of doubtful validity because of inadequate description and absence of a specimen. It is possible that some of these are synonyms of known species, but there is not sufficient information to establish their identity.

adamsi Pilsbry, 1896 : 112. Borneo.
chierchiana Mazzarelli & Zuccardi, 1892 : 13. Peru.
fusca Tilesius, 1809–13 : China and Japan.
laevigata Stimpson, 1855 : 378. China.
marginata and *marmorea* A. Adams, 1861 : 140. China.
punctatella Bergh, 1902 : 341. Philippines.
sinensis Sowerby, 1869 : China.
spuria Krauss, 1848 : 71. South Africa.
tarda Verrill, 1901 : 26. Bermuda.
tryonii Meinertzhagen, 1880 : 270. New Zealand.
venosa Hutton, 1875 : 279. New Zealand.
vexans Bergh, 1905 : 10. Amboina, East Indies.
Siphonota elongata Pease, 1860 : 24. Hawaii.
Siphonota grandis Pease, 1860 : 23. Hawaii.

Names given to juvenile forms whose status is doubtful :

parva Pruvot-Fol, 1953 : 38. Morocco. According to Marcus, 1958 : 10 this is a young *juliana*.

sorex Rang, 1828 : 57 (see p. 363).
Esmia griffithsiana Leach, 1847 : 266 (see p. 292).
vistosa Pruvot-Fol, 1953 : 37. Morocco.

Species named from shells only and unidentifiable from the descriptions : *bipartita*, *elegans* and *macula* Turton, 1932 : South Africa.

Name given to a probable hybrid :
Siphonota lobiancoi Mazzarelli, 1890 : 42 (p. 315).

(c) *History of the Genus*

Aplysia has been known from ancient times, the first authentic description being that of Pliny in the first century, A.D. He called it *Lepus marinus*, the Sea Hare, and described three kinds, two in the Mediterranean, and one, probably a *Dolabella*, in the Indian Ocean. He gave an account of the supposed poisonous qualities of this harmless mollusc. Other early writers compared it with a snail (Aelian) or a cuttlefish (Dioscorides).

In 1554 Rondelet included three kinds of *Lepus marinus* among the fishes in his *De Piscibus Marinis*, the first of which we now know as the Nudibranch *Tethys leporina*. He explained that it should not be confused with other fishes because " it is very poisonous and would be fatal to anyone who ate it ". But Gesner in 1551 had recognized that it was not a fish and placed it among the soft-bodied animals.

Redi in 1684 called it the Sea Slug and described its internal anatomy, and a century afterwards Bohadsch, a Bohemian fugitive living in Naples, published in 1761 a book on marine animals, describing two kinds under the name of *Lernaea*. He studied their habits and observed the discharge of purple and milk-white secretions. The opaline gland is sometimes called by his name. He realized that his *Lernaea* is related to the land snail.

British observers in the eighteenth century classified *Aplysia* amongst the Holothurians (Borlase, 1758) and the worms (Pennant, 1777).

In 1756 Linnaeus, in the 9th edition of the *Systema Naturae*, used *Lernea* (later adopted by Bohadsch as *Lernaea*) for the Sea Hare ; in the 10th edition (1758) he changed it to *Tethys*, mentioning two species, which he called *T. limacina*, with the habitat " Oceano Australi " and *T. leporina* (= *Lepus marinus*) in the Mediterranean; in the 12th edition, 1767 he changed the diagnosis, applied the name *Tethys* to the animal we know now as a Nudibranch and called the Sea Hare *Laplysia* (probably a printer's error), choosing as the type *L. depilans*[1]; finally in the 13th edition (1791) Gmelin corrected the spelling to *Aplysia*.

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[1] The word *Aplysia* means " that which one cannot wash " and was used by Aristotle for a sponge which could not be freed from grit and sand. Linnaeus chose the name arbitrarily. *Aplysia* came into common usage for the Tectibranch, *Tethys* for the Nudibranch. On the question of priority Pilsbry changed *Aplysia* to *Tethys*, thus making *Tethys* a genus of the family Aplysiidae and *Aplysia* a genus of the family Tethyidae. The International Commission on Zoological Nomenclature (Op. 200, 1954, **3**, 239–266) decided that the name *Aplysia* should be validated for the Tectibranch notwithstanding the Linnaean name in the 10th edition.

In the nineteenth century Lamarck (1822) classified the Aplysiidae near the Bulliidae. Cuvier in 1803 published a memoir on the genus "*Laplysia*" and gave the first full account of its anatomy, with good figures. European and especially Mediterranean species occupied the attention of Risso (1818), delle Chiaje (1828), de Blainville (1823), Milne Edwards (1847), Vayssière (1885) and Mazzarelli (1893), while the great voyages of the period brought specimens from foreign coasts in all parts of the world. Rang's monograph *Histoire naturelle des Aplysiens*, 1828 is still valuable for the descriptions and figures it contains. He accounts for 22 species of the genus *Aplysia*, which the modern systematist would reduce to seven or eight. He knew the three Mediterranean species *punctata*, *depilans* and *fasciata*, but did not realize that some species are circumtropical. In fact, this has always caused confusion in the genus. Local names have been given to world-wide species, thus multiplying the number of synonyms. Rang's species are *brasiliana*, *dactylomela*, *maculata*, *keraudreni*, *depilans*, *fasciata* and *punctata*.

At the end of the century the great monograph of Tryon appeared, Pilsbry contributing the section on the Aplysiidae, published in 1895 and 1896. Although largely a compilation from many authors it is the most comprehensive work existing on the family. He records at least 20 authentic species under the name *Tethys*, with numerous synonyms.

The expansion of our knowledge in the nineteenth and twentieth centuries is due to two groups of workers. The marine expeditions collected material from all the oceans, depositing it in the National Museums of the countries concerned. In some cases it was investigated, but often it was left unnamed. Some of these collections have been used by the author and provide interesting finds. For example, specimens of *Aplysia extraordinaria* from New South Wales, a species named by Miss Allan in 1932, have been in the Paris National Museum since 1874 and in the British Museum (Natural History) since 1883. *Aplysia morio*, described by Verrill from Bermudan examples in 1901, has been represented by a good specimen in the Swedish national museum since 1889.

The other group of workers consists of the local collectors who name their own species, often without access to known species for comparison, or to the literature. Frequently they failed to recognize world-wide species, with the result that synonyms were multiplied, young individuals were sometimes given specific rank and imperfect descriptions may make the species unrecognizable. Still more reprehensible was the naming of species from the dried shell alone, for shell shape is one of the most variable characters in the genus. To all who undertake to name new species, the author would recommend a study of p. 277 which gives the characters necessary for the identification of a species of *Aplysia*.

The seas of the world may be divided into ten areas according to the distribution of species of *Aplysia* (see Geographical Distribution, p. 377). This division is convenient but not arbitrary. Each area has been investigated by one or both of the two groups of zoologists mentioned above.

The three European species *punctata*, *fasciata* and *depilans* are perhaps best known, although synonyms are numerous. Work on them during the nineteenth century was initiated by Cuvier (1803 and 1817), continued by the compilations of de Blainville (1823 and 1825) and culminated in the beautiful and exhaustive monograph by Mazzarelli in 1893. In Great Britain only one species is indigenous, as Garstang (1890) recognized, but occasionally the larger continental species appeared on the south coasts and were recorded by Couch (1870) and Hunt (1877), and were identified by Grigg (1949). An account of the anatomy of *A. punctata* was published by the present author in 1921.

On the Atlantic coasts of North America the earliest systematist was Mörch, who in 1863 and 1875 named species from the West Indies. Thiele (1910) described, not very successfully, a few species from the same area, and Verrill (1901) gave the first account of a common, but hitherto unnamed, North American species, to which he gave the name *Aplysia morio.* Engel (1927 and 1936), in his work on the three species *dactylomela*, *cervina* and *parvula* from the West Indies, was the first to recognize that some species, such as *dactylomela*, are circumtropical. Further north Heilprin (1886) found and named *A. willcoxi* from New Jersey, and Sanford (1922) extended its range to New England.

In the West African region Risbec (1931) and Mme. Pruvot-Fol (1953) have studied the species from Morocco to Senegal, Odhner (1932) those of the Canaries and the author (1957) a collection from the coast of Ghana.

The South Atlantic has had little investigation. Bergh (1898) wrote one of his earliest papers on Opisthobranchs from the Plate, MacFarland (1909) and von Jhering (1915) described the Brazilian species, and more recently Dr. and Mrs. Marcus (1955) have published valuable papers on the Opisthobranchs of Brazil, two of which deal with Sea Hares, and have given much useful information on the living Aplysias to the author.

The Indian Ocean has always been a favourite collecting area for malacologists, particularly the Red Sea, and the shores of India, Ceylon, the Seychelles, Mauritius and Madagascar. Rüppell & Leuckart (1828) worked on Red Sea species, Quoy & Gaimard (1832), Adams & Reeve (1850), Martens (1880) and Eales (1944) on the island faunas, while for South Africa we have the publications of Burne (1906), Bergh (1908), O'Donoghue (1929) and Macnae (1955 and 1957). This region therefore has been well studied. Further east, China, Japan and the East Indies provided a happy hunting ground for the zoologist. Arthur Adams (1861) listed species from China and Japan, of which unfortunately there are no recorded specimens extant. Bergh's massive volumes on the mollusca of the Danish Expedition to Siam (1902), of Semper's *Reisen im Archipel der Philippinen* (1902 and 1908) and of the Siboga Expedition (1905) describe many, but not always authentic, species. Within the last few years Baba (1936, 1937, 1949 and 1952) has made excellent contributions to our knowledge of the fauna of Japan and Formosa.

The South Pacific, including Australia, New Zealand and Polynesia has been fairly adequately investigated by Angas (1867, 1877), E. A. Smith (" Alert ", 1884), Hedley (1916, 1918, 1923), O'Donoghue (1924, Abrolhos Isl.) and Allan (1932), the last of whom named from living material collected at Sydney the species *A. extraordinaria*, specimens of which had been in European museums for more than half a century. In New Zealand Meinertzhagen (1880) described that debatable species *A. tryonii*, the type of which has been lost. Hutton (1875 and 1882) described local species and Suter (1913) compiled a useful *Manual of the New Zealand Mollusca*. In Polynesia Eliot (1899), so well known for his studies of Nudibranchs, recorded some tectibranchs from Samoa, notably *nigrocincta* (= *parvula*) and *benedicti* (= *dactylomela*) and Gould (1852) contributed *A. pulmonica* from Hawaii. I agree with Bergh and Mme. Pruvot-Fol that Pease's species should be ignored, being based neither on adequate description nor on illustration. They are unrecognizable and no types exist. Ostergaard (1955) gave good figures of the species he considered to be Pease's *Syphonota elongata*, which may be *A. parvula*.

The Californian area produces some of the giants of the genus, but is not rich in species. Cooper (1863) described *A. californica*, which according to Macginitie attains a weight of 5 lb. 12 oz. MacFarland (1924) recorded *A. parvula* from this region. From the Gulf of California Bartsch & Rehder (1939) named *A. cedrosensis*, which was later found to be related to *A. depilans*, and Winkler (1955) described a black *Aplysia* without a sucker, which he named *A. vaccaria*.

The South American coasts from Columbia to Chile have been little worked, and few museums have specimens from this area. Lesson (1830), in collaboration with Rang, recorded *A. lessoni*[1] from Peru, d'Orbigny (1837) gave an account of several species, including three from Peru, which he called *A. nigra*, *A. rangiana* and *A. inca*, the second probably a variety of *juliana*, and the third, the type of which is in the Paris National Museum, an authentic species. Mazzarelli & Zuccardi's *A. chierchiana*, 1889 is a doubtful species.

Although small collections of species of *Aplysia* have been described, no one has hitherto attempted a world survey of the genus, based on adequate structural data. The fact that some species are circumglobal and others purely local makes such a survey both difficult and necessary.

(d) *Practical Notes*

Species of *Aplysia* can be recognized only by a combination of characters, the least reliable of which are colour and shape. Colour varies with food, age and habitat, and may fade altogether with preservation. Shape and size change greatly unless special precautions are taken during fixation.

It would help in identification, however, if collectors would record, in the living animal, the colour and markings, the nature of the mantle gland exudate (purple or white), the presence or absence of a sucker on the posterior end of the foot and the length of tail relative to the body.

A species of *Aplysia* cannot be said to be adequately described unless the following features have been investigated :

Size, appearance, mode of contraction, colour and markings, head, neck, foot, penis and penis sheath, parapodia, mantle and mantle aperture, anal siphon, mantle glands, opaline gland, shell, jaws, radula, caecum, nervous system.

In the descriptions which follow the features investigated for the diagnosis of species will be arranged in the following order.

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[1] Probably *keraudreni*.

1. External form (Text-fig. 1). Size, length, breadth and height. Shape and method of contraction. Nature of the skin, soft or leathery. Skin pigment and markings. Any known features of the living animal, e.g. swimming powers, curling up in a ball (Text-fig. 44*e*).

2. Head and neck. Relative size. Cephalic tentacles and oral extensions. Eyes. Rhinophores (Text-fig. 1).

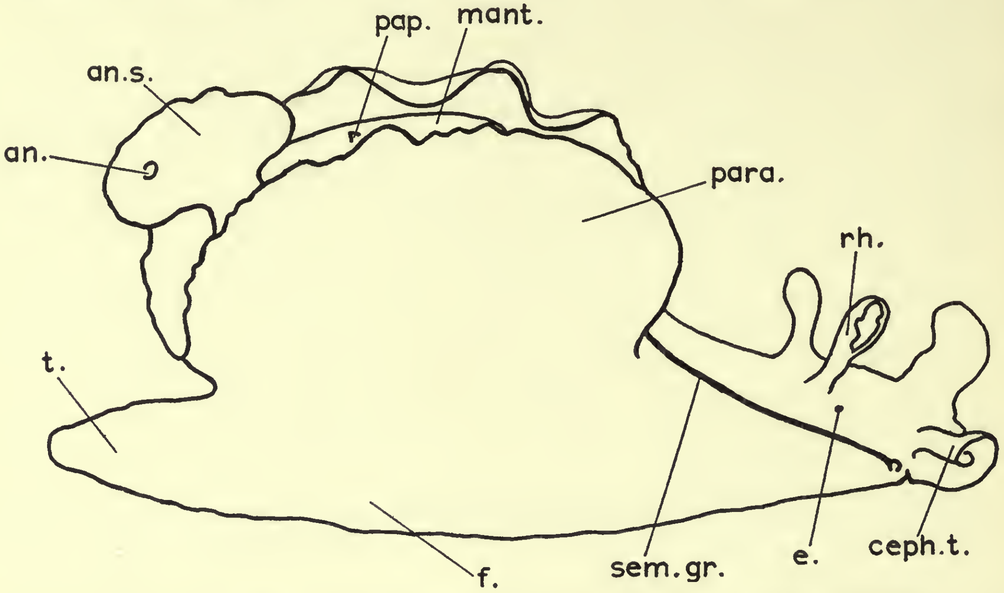

FIG. 1. *Aplysia dactylomela*. Lateral view to show main parts of its external structure. × $\frac{1}{3}$. For reference letters see p. 392.

3. Foot (Text-fig. 3). Soft or tough. Size, particularly relative breadth. Tail. Penis and penis sheath (Text-fig. 5, *b*, *c*). Parapodia, size, height, freedom and flexibility, anterior and posterior extent, relation to dorsal slit.

4. Mantle. Relative size. Shell foramen, anal siphon, overhang, mantle glands, and nature of exudate (Text-fig. 4).

5. Mantle cavity. Relative size. Ctenidium, opaline gland and aperture, genital aperture (Text-figs. 4, 5*a*).

6. Shell. Size, shape, quality, horny and calcareous layers, apex, " accessory plate ", anal sinus (Text-fig. 6).

7. Jaws. Size and shape. Jaw rods (Text-fig. 7, *e*, *f*).

8. Radula. Size and shape, rows of teeth and formula, denticulations and special features (Text-fig. 7, *a–d*).

9. Caecum. Size and shape. Other features of digestive system (Fig. 8, *b–d*).

10. Nervous system. Ganglia of the nerve ring. Visceral (supra-intestinal and visceral) ganglia (Text-fig. 8*a*).

Using *Aplysia dactylomela* and certain other species as examples, each feature used in the examination of a species is figured.

Colour. Colour means colour pattern as well as shade of colour. The colour is composed of at least two ingredients:

(*a*) Transparent colour, e.g. green, yellow, red, violet, rich brown, blue; this dissolves out or fades quickly in preservative, especially in alcohol.

(*b*) Granular colour, usually white, black or brown, which fades or dissolves gradually and may last for many years.

The soluble colour is said to be extracted from the weeds on which *Aplysia* feeds. Thus a young *A. punctata*, feeding on the red weed *Delesseria* and living in shallow water, is rose-red, coloured exactly like the weed—the *A. rosea* of Rathke. As it grows older the mollusc migrates shorewards to the brown weed zone and feeds chiefly on *Laminaria*, changing in colour to the rich olive brown of that weed. Finally the animal moves to the inter-tidal zone, and feeds on *Fucus*, darkening in colour as it does so. See Winkler 1959*a*.

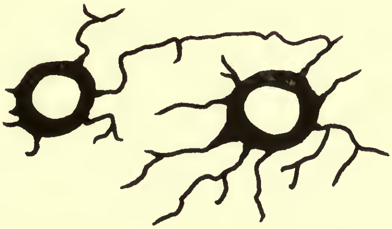

FIG. 2. *Aplysia dactylomela.* Two rings and reticulations, from a West African specimen. × $\frac{2}{3}$.

The basic colour may be modified by the formation of spots or flecks, sometimes in the form of light centres to regular or irregular rings of black granular pigment, as in *oculifera* and *dactylomela* (Text-fig. 2). More frequently the granular pigment consists of irregular bands and blotches of dark colour, alternating with areas of unpigmented or less heavily pigmented skin. In almost all species reticulations of granular pigment are present, and there may be white granules, probably of a calcareous nature, the latter occurring also on the surface of the digestive gland. Species of *Aplysia*, however, rarely show the pattern of "ocelli", with red or turquoise centres, so common in the Notarchinae.

Foot (Text-fig. 3, *a–c*). This may be broad, of medium width or narrow (see Criteria, p. 286). There is usually a rounded or pointed tail, not as long as in *Stylocheilus*. In the subgenus *Aplysia* the posterior end of the foot forms a temporary sucker owing to the abundant secretion of the posterior pedal mucus-forming glands.

Penis and penis sheath (Text-fig. 5, *b*, *c*). These are derivatives of the foot. The former may be short and broad, pike-shaped or long and filiform. The sheath is composed of two parts, the proximal portion near the aperture being strongly muscular, with longitudinal ridges internally. The distal portion, from which the penis springs, is enlarged and smooth-lined in most species, but in the subgenus *Aplysia* it is greatly enlarged and its lining bears numerous rounded swellings or warts, each capped by curved spines, probably chitinous in nature.

Parapodia (Text-fig. 1). The parapodia are lateral upgrowths of the foot in the visceral region; they vary greatly in extent and flexibility. In most species they are natatory, widely spaced anteriorly and meeting or joining posteriorly. When joined high up, as in the subgenera *Pruvotaplysia* and *Aplysia,* they shut in the mantle cavity behind, forming a mantle cavity pocket. When joined or meeting low on the tail, as in *Neaplysia* and *Varria,* the mantle cavity is open both in front and behind, and the floor may be extended backwards as a flat platform. The anal siphon, usually erect, can then be directed backwards as in the allied genus *Syphonota.*

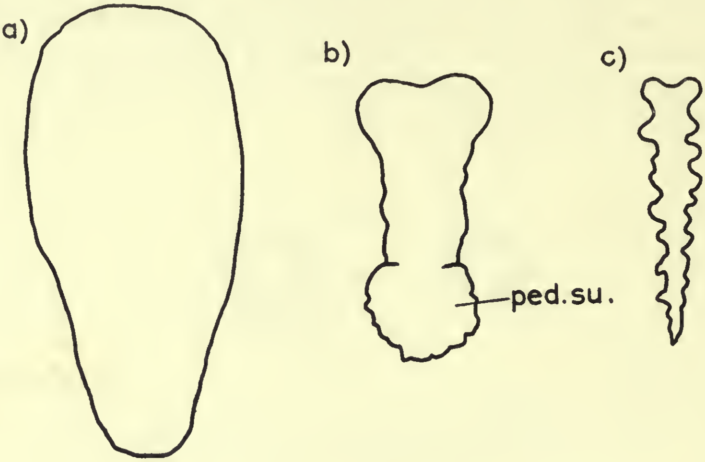

Fig. 3. The foot.

(*a*) *Aplysia dactylomela.* Foot sole broad, with rounded tail.
(*b*) *A. juliana.* Foot broad, with anterior side wings and posterior sucker.
(*c*) *A. parvula.* Foot narrow, with pointed tail, contracting to form a characteristic wavy outline laterally. All × $\frac{2}{3}$.

Mantle (Text-fig. 4). The mantle in all adult Aplysias is reflected upwards over the shell, enclosing the latter in a shell sac. In the very young animal the shell is exposed, but during growth the mantle turns up over its edge, the aperture becoming progressively smaller with age. In *Pruvotaplysia* and *Aplysia* this aperture remains as a round or oval flat hole, contractile in *Aplysia* so that it may close or nearly close. In *Neaplysia* and *Varria* the aperture is small, papillate or absent altogether. Thus the condition of the mantle aperture may vary considerably according to the degree of contraction of the mantle aperture.

Opaline gland (Text-figs. 5*a*, 9). The opaline gland, or gland of Bohadsch, is situated on the floor of the mantle cavity postero-lateral to the common genital aperture. There are two main types in the genus:

(*a*) The simple gland, probably primitive, in which the gland is composed of large, flask-shaped cells, each with its own aperture to the mantle cavity, s.g. *Pruvotaplysia, Aplysia,* etc.

(*b*) The compound gland, in which the gland cells combine to discharge by a single duct into the mantle cavity, the gland hanging from the floor into the haemocoele like a bunch of grapes on a vine. This type occurs in *Neaplysia* and in about half of the members of *Varria*.

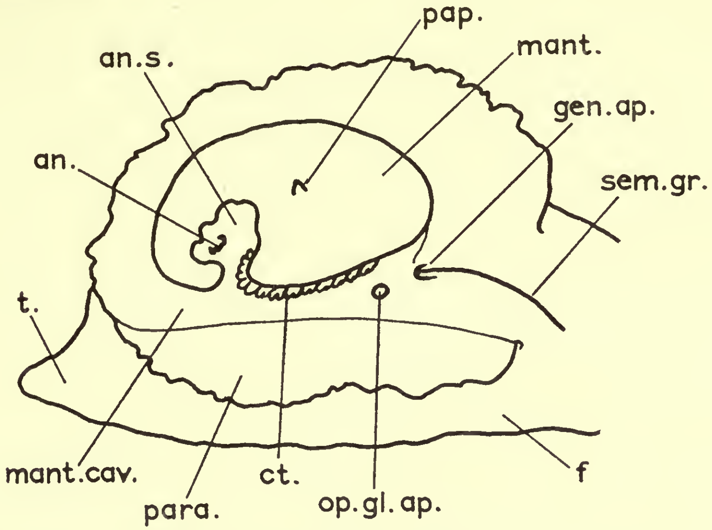

FIG. 4. *Aplysia dactylomela.* Lateral view of the posterior region to show the mantle cavity and its contents. The right parapodium has been reflected. × 1.

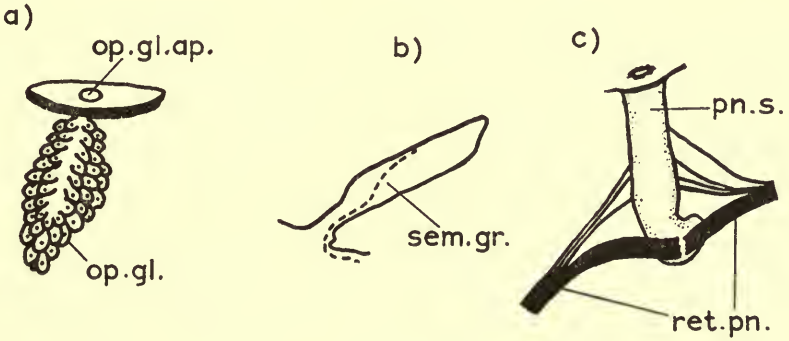

FIG. 5. *Aplysia dactylomela.*

(*a*) Opaline gland in longitudinal section to show the central chamber into which the gland cells open, and the single aperture to the mantle cavity. This is the compound uniporous type. × 2.

(*b*) Penis. The sperm groove is indicated by a dotted line and twists spirally round the penis. × 2.

(*c*) Penis sheath seen from the ventral side to show the arrangement of the retractor muscles. × $\frac{2}{3}$.

There is a tendency, in species with simple glands, e.g. *cornigera, keraudreni, oculifera,* for a few of the gland vesicles to unite, while others remain separate, giving one aperture, usually the anterior, larger than the others, with a cluster of small ones. This transition type is regarded as simple and multiporous.

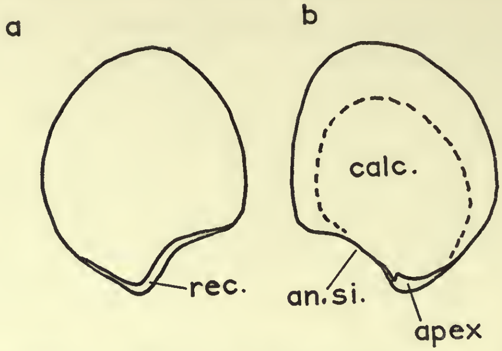

FIG. 6. *Aplysia dactylomela.* Shell, from an African specimen 112 mm. long. × $\frac{2}{3}$.
(*a*) Dorsal view, showing the recurved edge.
(*b*) Ventral view, showing the apex. The dotted line represents the extent of the calcareous layer.

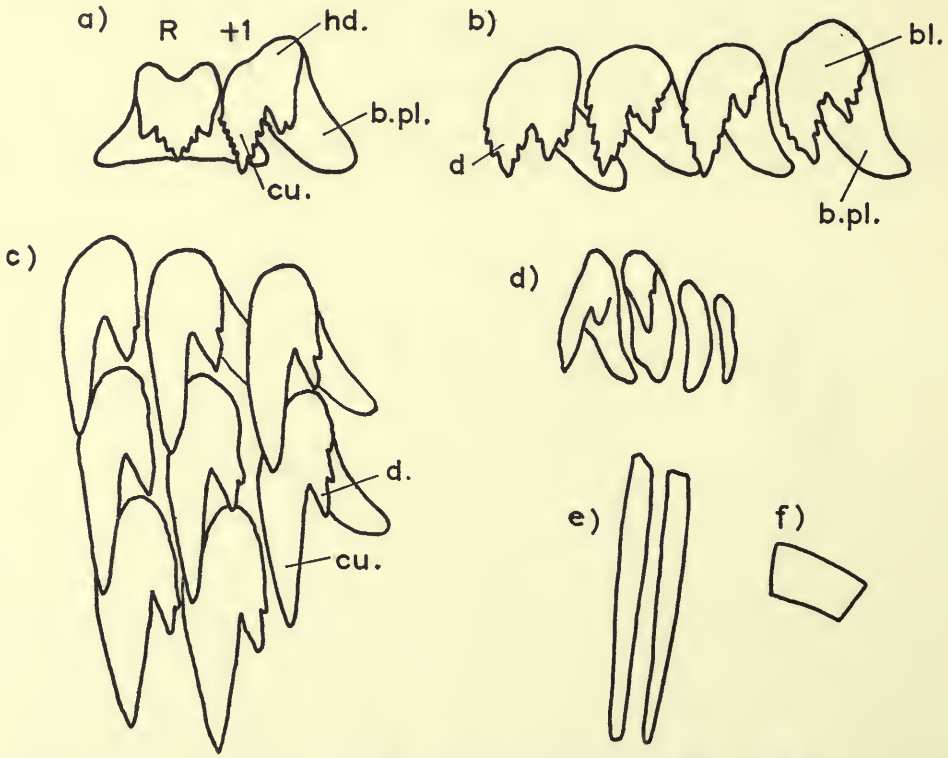

FIG. 7. *Aplysia dactylomela.* *a–d* teeth from the radula. × 84.
(*a*) Rhachidian and first lateral of one side.
(*b*) First to fourth laterals.
(*c*) Part of three rows of laterals from the middle of a side to show the straight overlapping cusps. Only three of the basal plates are figured.
(*d*) Four outermost laterals.
(*e*) Jaw rods. × 168.
(*f*) Jaw. × $\frac{2}{3}$.

Shell (Text-fig. 6). The shell is a variable feature in *Aplysia* and is usually unreliable for diagnosis of the species when considered alone. This is to be expected, since it is enclosed in the mantle and can only be regarded as degenerate. It consists of a horny exterior which is delicate and flexible, covering a smaller and often fragmented calcareous layer. When dried the horny portion alone is left as a rule, and this is not representative of the shell as a whole. Sowerby's numerous species, founded on the dried shell, are therefore of little value in many cases. Some species, e.g. *juliana*, have geographic races characterized by the shape of the shell.

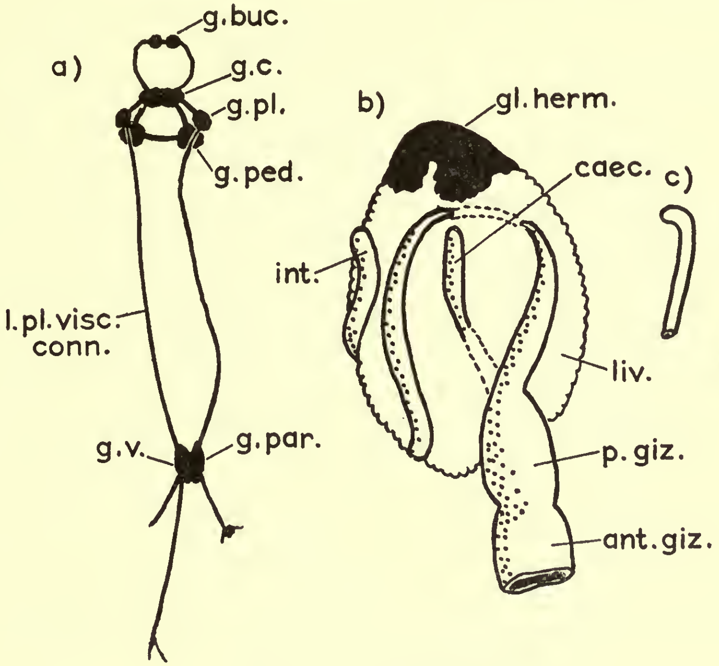

Fig. 8. *Aplysia dactylomela.*

(*a*) Nervous system in dorsal view. The cerebral ganglia are completely fused, also the supra-intestinal and visceral. × 2.
(*b*) *A. dactylomela.* Visceral mass in ventral view to show the position of the caecum, straight in this species. The hermaphrodite gland occupies the posterior tip of the visceral mass. × 1½.
(*c*) Caecum of *A. punctata* for comparison.
(*d*) Caecum of *A. juliana.*

The genus has three types of shell :

(*a*) Shell with a persistent involuted or spiral apex, strongly concave, e.g. *parvula* (Text-fig. 11*b*).

(*b*) Shell with apex flattened to form a rectangular plate, described incorrectly by Cooper (1863) as an " accessory plate ", e.g. *californica* (Text-fig. 12, *a*–*c*).

(*c*) Shell without spire or accessory plate, usually with recurved but not flattened apex. Most species (Text-fig. 6, *a*, *b*).

Radula (Text-fig. 7, *a–d*). The radula is well developed and consists of many rows of teeth, with a formula X.1.X, where X varies from about 15 in small species to more than 80 in large ones. All the laterals are basically similar, with the exception of from three to six of the outermost teeth, which are vestigial.

Caecum (Text-fig. 8, *b–d*). The caecum appears on the surface of the digestive gland at its tip only, or for part of its length. There are three types, a straight caecum lying flat on the surface (*dactylomela*), a caecum curved at the tip and just breaking surface (*punctata*) and a much curved, crozier-shaped or spiral caecum, with the tip hidden (s.g. *Aplysia*).

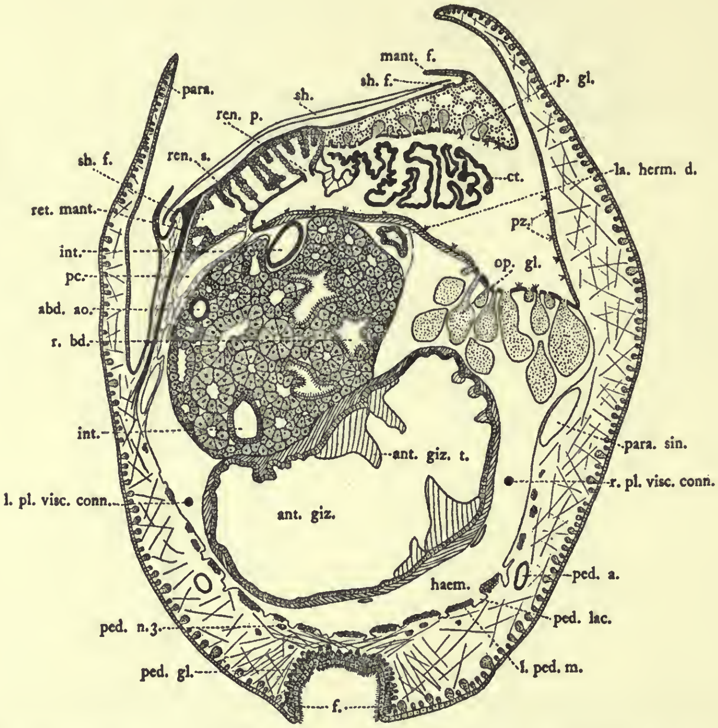
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FIG. 9. *Aplysia punctata*. Transverse section of a young individual through the visceral hump, above which lie the mantle cavity, mantle and shell. The mantle fold is just beginning to enclose the shell. Note the simple multiporous type of opaline gland. × 10·5. Reproduced from L.M.B.C. Memoir 24.

Nervous system (Text-fig. 8*a*). The nerve ring exhibits differing degrees of fusion. In the most primitive species (*Pruvotaplysia*) the cerebral, pedal and pleural ganglia are rounded and distinct, the cerebral and pedal ganglia with commissures. In most species the cerebral ganglia are contiguous within a connective tissue sheath, or completely fused into a flat band. The pleural and pedal ganglia are always separate, but may lie close together. The visceral pair (supra-intestinal or parietal and infra-intestinal plus visceral ganglia) are either distinct or fused, but may vary with age. They are, however, always on long pleuro-visceral cords and lie close to the large hermaphrodite duct.

Killing and Fixation

Aplysia is a strongly contractile animal and may shrink to as little as one-third of its length when preserved. Much of this shrinkage may be avoided by narcotization before fixing. Three methods are given.

1. Sprinkle menthol crystals on the surface of the sea water in which the animals are relaxed in a vessel of convenient size. When immobile, after about 12 hours, fix in 2% chromic acid for 24 hours. Wash in water for 24 hours. Preserve in 5% formalin or formol alcohol.

2. Macginitie's method. Dissolve 75 grams of magnesium chloride and 10 grams of urethane in one litre of distilled water. Place the animal in a vessel with sea water and add the above solution by the drip string method. When immobile proceed as in 1.

3. If chromic acid and the other ingredients are not available, fix in formol alcohol or formalin.

Formalin hardens the tissues, and in time dissolves the calcareous lining of the shell, but it preserves much of the pigment. Alcohol does not harden so much, but extracts the colour rapidly.

Dissection

It is most important that examination of internal structures should be done without disturbing the external appearance of the specimen any more than is necessary. The internal parts it is necessary to examine are the shell, penis and penis sheath, jaws, radula, opaline gland, visceral ganglia, nerve ring and caecum.

Shell. The mantle aperture should be preserved. Make a cut near the periphery of the mantle anteriorly and continue in a crescent along the *left* side. When the cut has extended as far as the shell apex, the shell can usually be lifted out gently by raising the flap of mantle tissue. After inspection the shell can be replaced.

Internal Structures. Examine from the ventral side. Make a longitudinal cut in the middle line of the foot and continue forwards through the anterior pedal groove to the mouth aperture. Press the cut edges of the foot apart and find the opaline gland on the left (animal's right) immediately to the left of the genital duct. To the right of the genital duct lies the large colourless cephalic artery and between the latter and the globular Swammerdam's vesicle are the supra-intestinal (parietal) and visceral ganglia, side by side, and linked by the pleurovisceral cords with the nerve ring around the oesophagus anteriorly. To expose them the digestive gland and gizzard may have to be turned to the right.

To find the caecum, turn the animal with the anterior end nearest to you (Text-fig. 8*b*). Remove the covering of connective tissue from the visceral mass, and note the positions of the gizzard (right), hermaphrodite gland (posterior) and the course of the intestine (left). Within this triangle the caecum comes to the surface, either lying flat on the digestive gland, or exposing its tip. It may be traced back to the stomach by separating the digestive gland tissue.

Nerve ring (Text-fig. 8*a*). This consists of cerebral, pleural and pedal ganglia on each side, and from the cerebral ganglia connectives run to a pair of buccal or stomato-gastric ganglia on the ventral side of the oesophagus, between it and the buccal mass. Isolate these ganglia from the buccal mass and oesophagus by cutting the nerves, leaving the ganglia attached to the ring by their cerebro-buccal connectives. Sever the oesophagus close to the buccal mass, and slip it through the nerve ring, which can then be examined. Push the buccal mass forward, severing it from the body around the mouth aperture.

Jaws and radula. Boil the buccal mass in a porcelain dish in 5% Potassium hydroxide until the jaws and radula can be removed from the softened muscle. A small piece cut off the edge of the jaw is sufficient for the examination of the jaw rods. The radula should be brushed gently to remove the radular membrane from the posterior rows of teeth. After examination under the microscope the separated parts can be placed in a small tube to be put into the jar containing the specimen.

Penis and penis sheath. These lie alongside the buccal mass, on its left side when viewed ventrally. The sheath should be slit open longitudinally, so that the penis protrudes ; it can then be examined *in situ*.

After examination the specimen, closed up again along the foot incision, resumes its original shape.

(e) *Criteria Employed in the Description*

Owing to the vagueness of such terms as large, broad, etc. it has been found necessary to adopt limits of size, according to the following criteria :—

Body size : Large—More than 150 mm. preserved, alive 300 mm. or more.
Medium—75 to 150 mm. long.
Small—Up to 75 mm. long.

Foot : Broad—More than 25% of the body length.
Medium—15% to 25% of the body length.
Narrow—Below 15% of the body length.

Shell : Broad—Length less than 1½ times the breadth.
Narrow—Length at least 1½ times the breadth.

It should be noted that the above limits are a guide only and are not absolute.

In the account of the species which follows, a full list of synonyms, as far as is ascertainable, with references, comes after each specific heading. At the end of the description the specific characters necessary for identification are given. The list of references to the species excludes those given in the synonymy. Full titles of papers appear at the end.

2. DESCRIPTIONS OF THE SPECIES

Subgenus **Pruvotaplysia** Engel, 1936

Aplysia (Pruvotaplysia) parvula Guilding in Mörch, 1863 : 22

Text-figs. 10 and 11

SYNONYMY : *allochroa* Bergh, 1908 : 4 (*non* O'Donoghue, 1929).
anguilla Cuming, MS. Sowerby, 1869 : pl. 6, shell only.
atromarginata Bergh, 1905 : 8.
australiana Clessin, 1899 : 22, shell only.
concava Sowerby, 1869 : pl. 6, shell only.
intermedia Farran, 1905 : 351.
japonica Sowerby, 1869 : pl. 5, shell only.
lobata Bergh, 1908 : 8 (or this may be a young *dactylomela*).
monochroa Bergh, 1908 : 13.
nigrocincta Martens, 1880 : 307.
norfolkensis Sowerby, 1869 : pl. 10, shell only.
orientalis Sowerby, 1869 : pl. 5, shell only.
paeteliana Clessin, 1899 : 96, shell only.
peasei Pilsbry, 1895 : 95 as *Tethys*.
? *peregrina* Thiele, 1925 : 281.
rosea ; Sowerby, 1869 : pl. 6, shell only (*non* Rathke, 1799).
sieboldiana Clessin, 1899 : 54, shell only.
subquadrata ; Sowerby, 1869 : pl. 9, shell only (*non* Gould).
? *trigona* Sowerby, 1869 : pl. 4, shell only.
Aplysiopsis juanina Bergh, 1898 : 483.
? *Syphonota elongata* Pease, 1860 : 24.
? *Syphonota punctata* Pease, 1868 : 77.

It is possible that Meinertzhagen's *tryonii* (1880 : 270) belongs to this species, but the description is inadequate and the type has been lost. A specimen in Wellington Museum labelled *tryoni* proved to be *parvula*.

Krauss in 1848 gave an imperfect description but no figure of a " spurious *Aplysia* " from South Africa, to which he gave the name *Aplysia spuria*. He compared it with Rang's *maculata* and thought it had no posterior tentacles, hence the name *spuria*. Macnae (1955 : 235) claimed that this is the species later called *parvula*, and that the name should be changed to *spuria*. There is considerable doubt regarding Krauss's species, and the type has disappeared from the Swedish National Museum in Stockholm. Application was accordingly made to the International Commission on Zoological Nomenclature (April 1957) to validate the specific name *parvula* Mörch, 1863, and suppress *spuria*. This was confirmed in Opinion 560, 1959.

Pease's species should be ignored, but Ostergaard (1955) has used the name *Tethys elongata* for a Hawaiian species, which may or may not be *parvula*. Unfortunately I have been unable to obtain a specimen.

Distribution. The species is circumtropical in distribution, occurring in warm seas from approximately 40° north latitude to 40° south latitude. It has been recorded in the western North Atlantic from Florida to Brazil and from many islands in the West Indies ; in the eastern North Atlantic from Morocco, the Azores, Madeira and Senegal ; in the Indian Ocean from the Gulf of Aden, India, Ceylon and Mauritius to the Cape ; in the Pacific Ocean from Japan, China, the East Indies to Samoa, the Hawaiian Islands, the Society Islands, Australia and New Zealand ; and in the eastern Pacific from California, South California and the west coast of South America.

Material examined. Numerous specimens from all parts of the world.

This beautiful but variable little *Aplysia* was described by Mörch from two specimens collected on the island of St. Thomas in the Lesser Antilles, West Indies. He stated that he had seen a shell of the species in the British Museum (Natural History) from St. Vincent, named by Guilding *A. parvula*, but no trace of that portion of Guilding's manuscript referring to this species can be found. Mörch noted its resemblance to *A. longicornis* Rang (= *punctata* Cuvier, 1803). *A. parvula* was later found in many other parts of the world and appears under local names, such as *norfolkensis*. Engel (1927 and 1936) was the first to show that the species is circumtropical. In 1931, Risbec, describing a specimen from Morocco, gave a figure of the shell of the young animal with its spire, sketched the characteristic wavy contraction of the edges of the foot and the distinct, rounded ganglia of the nerve ring. Mme. Pruvot-Fol recognized the primitive characters of the species, and in her honour Engel (1936) suggested the subgeneric name *Pruvotaplysia*. Baba (1949, pl. 3), published an excellent coloured reproduction of the living animal belonging to the variety *nigrocincta*. In 1956 he described the egg strings as pink or yellow, with only two to three eggs in each capsule.

Description of the Species

Small or very small Aplysias, rarely reaching more than 60 mm. in length, although the tail may elongate still further. Body rounded and neat, typically higher than wide when contracted, but elongated and flexible when moving (Text-figs. 10 and 11*a*). Skin soft. Colour very variable—purplish black, dark brown, tan, yellow, greenish grey or green, speckled with white or cream. The variety *nigrocincta* has the mantle foramen, siphon, parapodia, rhinophores and cephalic tentacles, anterior border of the foot and tip of the tail bordered with black and orange. Another variety from Madagascar, now in the Swedish National Museum, has scattered papillae on the sides of the body, similar to those figured by Quoy & Gaimard in their *A. tigrina* (= *tigrinella* M. E. Gray, 1850, = *maculata* Rang, 1828, according to Macnae, 1955).

Head small and neat, neck long. Cephalic tentacles strongly contractile, but when expanded large, dilated, sometimes fimbriated, usually free from the mouth slit. Eyes plain, usually on light patches. Rhinophores small, slender, acute, split for two-thirds of their length, fairly close together. Both the cephalic tentacles and the rhinophores are black in the folded portions.

Foot narrow, pale, with slender, pointed tail; the edges when contracted have a wavy border. Penis (Text-fig. 11*c*) broad at the base, short and tapering, blunt-tipped, sheath smooth-lined. Parapodia short, not very mobile, rounded anteriorly, widely open, fused posteriorly, forming a moderately high wall round the mantle cavity. MacFarland (1924) described them as large and fleshy in Californian specimens.

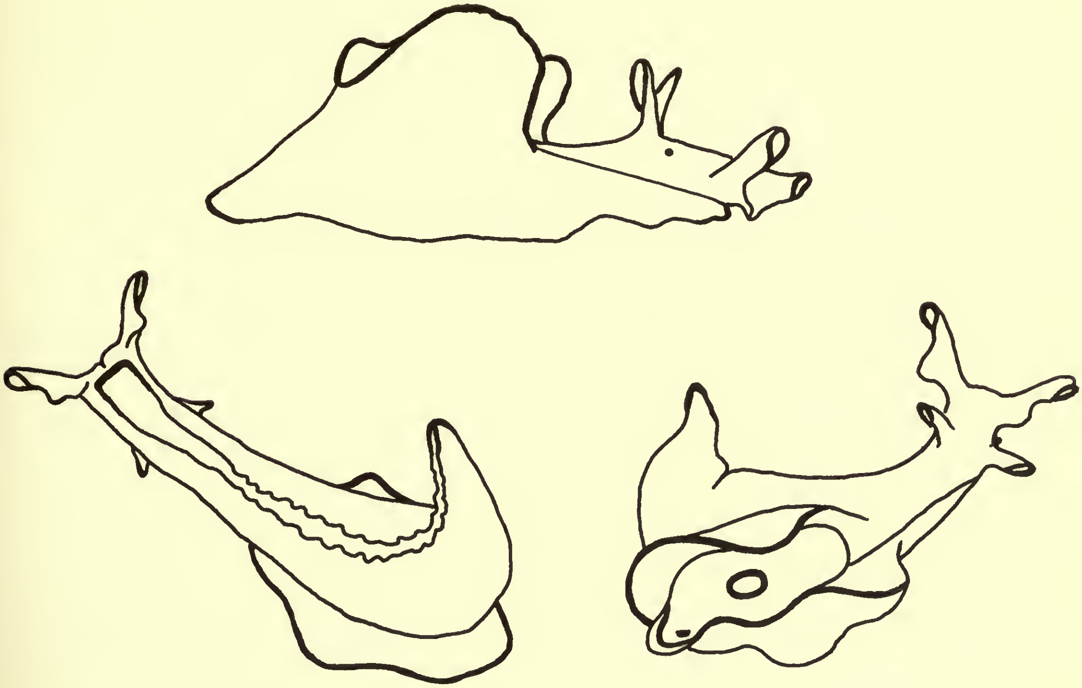

Fig. 10. *Aplysia parvula.* Lateral, ventral and dorsal views of living specimens, from colour photographs taken by Dr. H. Lemche at Cronulla, New South Wales. The heavy lines indicate the black edges of the cephalic tentacles, rhinophores, anterior and posterior borders of the foot, mantle aperture, anal siphon and parapodia. × 1½.

Mantle thin, with a large oval foramen, at least one-third the width of the shell. Anal siphon of moderate size. Purple glands well developed.

Mantle cavity closed behind. Ctenidium small and compact. Opaline gland simple, multiporous, though some ductules may coalesce anteriorly. Genital aperture rather far forward, covered by the mantle overhang, smooth, crescentic.

Shell (Text-fig. 11*b*) large for the size of the animal, oval or almost circular, strongly concave, thin and delicate in the horny portion, but well calcified beneath, especially near the apex, which is hard, incurved, often with a distinct spire especially in young specimens, and a small projecting, thickened hood. This is the only species of *Aplysia* which may retain the spiral apex in the adult, although it is not unusual for juveniles of other species to exhibit this feature (cf. Marcus, 1955 : pl. 4, fig. 29, for *juliana*). Solution of the calcareous portion of the shell, however, reduces the apex considerably.

Jaws triangular. Rods densely packed, slightly curved or straight.

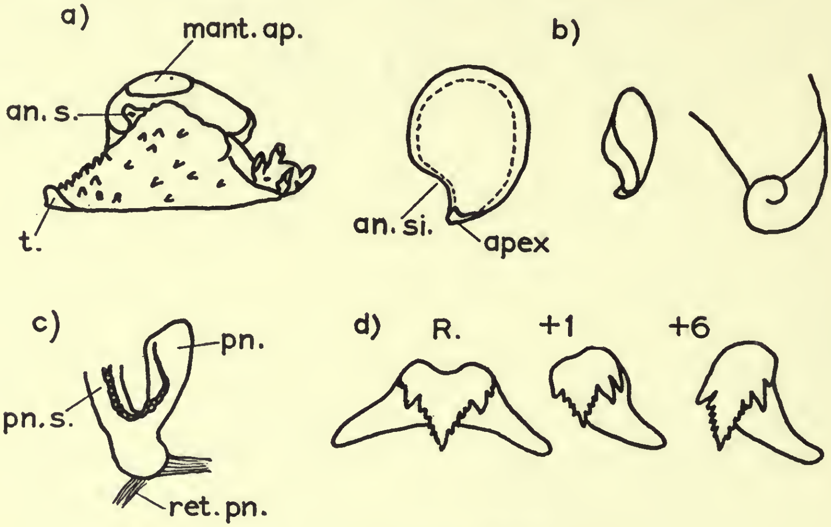

FIG. 11. *Aplysia parvula.*

(*a*) Right lateral view of a contracted specimen from the Swedish National Museum, Stockholm. The specimen shows the high humped appearance of the contracted animal, but is unusual in that the sides of the body bear scattered papillae, which are more crowded on the tail to form a small keel. × 1½.

(*b*) Shell in ventral and lateral views, and enlarged in ventral view, from a young specimen figured by Risbec, 1931, to show the spiral apex. The dotted line represents the limit of the calcareous lining.

(*c*) Penis sheath opened longitudinally to show the short broad penis and sperm groove. × 6½.

(*d*) Radular teeth. Rhachidian, first and sixth laterals. × 80.

Radula (Text-fig. 11*d*) with few rows and a small number of teeth in a row, a typical formula being 30 × 16.1.16. Rhachidian tooth with unusually short but wide, incised basal plate, finely denticulate main cusp and one or two stronger denticles laterally. First lateral with rather long cusp, similarly denticulate, the large lateral denticles increasing in size further along the row, but the cusp remaining shorter than the plate. From three to four outermost teeth degenerate.

Caecum short, just breaking surface on the digestive gland. The hermaphrodite gland is pushed up tightly into the spire of the shell.

Nervous system primitive in that all the ganglia of the nerve ring are distinct, the pleurovisceral cords are short and the visceral ganglia separate.

SPECIFIC CHARACTERS

Aplysias of small size, neat appearance. Elongated in shape, but of high aspect when contracted. Foot narrow, with wavy borders when contracted, parapodia joined high up posteriorly. Penis short, with blunt tip, sheath lining smooth. Mantle with large oval foramen. Purple secretion from the mantle glands. Opaline gland simple, multiporous. Shell relatively large, deeply concave, with strongly inflected apex or with distinct spire. Radula with not more than 20 lateral teeth, rhachidian tooth with wide but very short basal plate. All the nerve ganglia distinct, pleurovisceral cords short. Colour variable, but an edging of black and orange pigment is characteristic of the variety *nigrocincta*.

Circumglobal in warm seas.

References (*see also synonyms*)

Allan, Joyce, 1932 : 424, as *norfolkensis*.
Angas, 1877 : 190, as *norfolkensis*.
Baba, 1937 : 208.
Baba, Hamatani & Hisai, 1956 : 216 (breeding habits).
Burne, 1906 : 56, 57, as *nigrocincta* and *elongata*.
Cotton & Godfrey, 1933 : 96, as *norfolkensis*.
Dall, 1885 : 24.
Dall & Simpson, 1902 : 366.
Edmonson, 1933 : 154, as ? *Tethys elongata*.
Eliot, 1899 : 513, as *nigrocincta*.
Engel, 1927 : 90 ; 1936*a* : 15.
Haas, 1920 : 56.
Macnae, 1955 : 235, as *spuria*.
MacFarland, 1924 : 398, as *Tethys*.
Ostergaard, 1955 : 114, as *elongata* ?.
Pilsbry, 1895, as *parvula*, *anguilla*, *elongata*, *peasei*, *japonica*, *nigrocincta*, *norfolkensis*, *concava*, *orientalis* and *trigona*, all under *Tethys* : 83, 112, 93, 95, 106, 107, 99, 100, 104, 112.
Pruvot-Fol, 1932 : 4 ; 1933 : 104 ; 1935 : 254 (suppression of Bergh's *Aplysiopsis*).
Risbec, 1931 : 74.
Suter, 1913 : 545 and pl. 36, fig. 6, as *T. tryoni*, which is probably *parvula*.
Thiele, 1910 : 123.

Aplysia (Pruvotaplysia) punctata Cuvier, 1803 : 295

(Fully illustrated by Eales, 1921, q.v.)

SYNONYMY : *albo-punctata* Deshayes, 1853 : 59.
cuvieri and *cuveriana* delle Chiaje, 1822 : 41.
?*depilans ;* Pennant, 1812 : 42.
depilans minor Barbut, 1783 : 32, pl. 3, fig. 5.
dumortieri Cantraine, 1840 : 71.

ferussaci Rang, 1828 : 66, pl. 19.
guttata Sars, M., 1840 : 213, Taf. 7.
hybrida Sowerby, J., 1806 : pl. 53.
longicornis Rang, 1828 : 66.
marginata de Blainville, 1823 : 326 ; Rang, 1828 : 59 ; Philippi, 1844 : 98.
mustelina? Davies in Pennant, 1812 : 29, pl. 22.
nexa Thompson, 1845 : 313.
nigromarginata Risso, 1818 : 374.
[1]*rosea* Rathke, 1799 : 85 ; Odhner, 1907 : 16 and 61 ; 1922 : 6 (*non* Sowerby, 1869) (juv.).
stellata Risso, 1818 : 374.
subquadrata Gould in Sowerby, J., 1806 : 111, pl. 53.
unicolor Risso, 1818 : 374.
varians Leach, 1847 : 268 and 1852 : 33.
virescens Risso, 1826 : 42.
[2]? *Esmia griffithsiana* Leach, 1847 : 268 (juvenile) (spelt *griffithsiae* by M. E. Gray, 1850).

DISTRIBUTION. Atlantic coasts from Greenland, Norway and the Baltic to the Canary Islands and the Mediterranean. The common British species.

MATERIAL EXAMINED. Numerous specimens from British and French coasts and the Mediterranean.

A good figure was given by Rang (1828, pl. 18). A full account of the anatomy was published by the author (1921).

Aplysias of moderate size, reaching 200 mm. when alive, but usually smaller. Body capable of great elongation, especially in the head and neck regions, contracting to the " sitting hare " position. Colour when mature a rich velvety olive brown to olive green, resembling the weed *Laminaria* and *Fucus* respectively, often accompanied by black spots and reticulations, irregular greyish flecks or white blotches formed by the fusion of clusters of unpigmented spots. When preserved the soluble brown colour is extracted, leaving black, grey and white. Young specimens about 6–10 mm. long are rose red, the animals feeding at this stage on red seaweeds such as *Delesseria*. This was described by Garstang in 1890. Skin soft but firm.

Head and neck long and narrow. Cephalic tentacles short with rounded extensions to the mouth slit. Eyes plain, on clear, circular areas of skin. Rhinophores elongated, tapering, slit half-way.

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[1] Odhner (1907) pointed out that *rosea* should have priority over Cuvier's *punctata*. The International Commission on Zoological Nomenclature, Opinion 355, **11**, 91–102, Aug. 1955, " suppressed the name *rosea* Rathke, 1799, and placed the specific name *punctata* Cuvier, 1803, as published in the combination *Aplysia punctata* on the Official List of Specific Names in Zoology."

[2] It is not clear whether Leach's specimen was a juvenile *punctata* or *depilans*. Although Leach's Mollusc collection was given to the B.M. (N.H.) and the specimens were re-named by J. E. Gray, his *Esmia* cannot be found.

Foot narrow, colourless, with rounded anterior edges and long pointed tail, adapted for crawling up the stipes of *Laminaria*, the lateral borders curling towards each other. Penis spatulate, flat, sheath smooth-lined, with a single retractor muscle. Parapodia mobile, thin, natatory, smooth-edged but capable of forming a fluted pattern when the animal is feeding on a frilled weed such as *Chondrus crispus*, joined high up posteriorly, thus closing the mantle cavity behind.

Mantle thin with a flat circular or oval aperture, tall, tubular anal siphon and well developed purple gland.

Mantle cavity not large, opaline gland simple, multiporous, but small groups of vesicles may fuse. Genital aperture smooth, pigmented.

Shell delicate, transparent, moderately concave, rounded anteriorly, apex downturned but not spiral, anal sinus very shallow, dorsal border of apex reflected. In the young, the spire of the shell, as in many juvenile Aplysias, is well formed, cf. Mazzarelli, 1893 : pl. 12.

Jaw rods of moderate length, straight, but tapering and slightly bent at the tip.

Radula small, not heavily chitinized. About 40 rows and a formula 15–18.1.15–18. Rhachidian tooth with broad, fairly short basal plate, incised both anteriorly and posteriorly, cusp narrow near the point, a little longer than the plate, bearing a few small neat denticles and two pairs of large basal ones, the penultimate denticle being the larger of the two. First lateral with narrowing, almost triangular basal plate, broad head, narrow cusp repeating the rhachidian pattern laterally. The larger denticle may split into two or more. Along the row the plates remain narrow, the heads and cusps become more slender, but the cusps do not exceed the length of the plates, the denticles increase in size, particularly the lateral basal ones. The two outermost teeth are small and vestigial.

Caecum short, only the curved tip visible on the surface of the digestive gland.

Cerebral, pleural and pedal ganglia rounded and distinct. Visceral group (right parietal and visceral) also separate.

Specific Characters

Of moderate size, with rich velvety olive brown or olive green colour, with or without black reticulations and clear areas, and soft firm skin. Head and neck long, but contracting back to the visceral hump to give a " sitting hare " appearance. Foot narrow, unpigmented, with pointed tail. Penis broad, spatulate, flat. Parapodia natatory, joined high up posteriorly. Mantle with flat aperture. Purple secretion. Opaline gland simple, multiporous. Shell delicate, with weak anal sinus, inturned apex, but no spire. Radula small, with neat regular denticles and a formula 40 × 18.1.18. All the ganglia of the nerve ring rounded and separate, as are also the visceral ganglia.

Eastern North Atlantic.

References (*see also synonyms*)

Colgan, 1911 : 21.
Dautzenberg & Fischer, 1925 : 29.
Eales, 1921 : 1–84.
Engel, 1934 : 85–89.

Férussac, 1821-22 : xxx.
Fischer-Piette, 1932 : 14.
Fleming, 1828 : 291.
Garstang, 1890 : 401.
Grigg, 1949 : 795.
Guérin-Menéville, 1843 : 20.
Hertling, 1935 : 103.
Hoffman, 1926 : 7.
Jeffreys, Gwyn, 1866 : 81 ; 1869 : 1.
Locard, 1886 : 59.
Mazzarelli, 1889 : 582 ; 1893 : 25.
Norman, 1890 : 69.
Pilsbry, 1895 : 70, as *Tethys*.
Saint Loup, 1888 : 1010.
Sars, G. O., 1878 : 213.
Sars, M., 1878 : Tab. 12, fig. 18.
Sykes, 1905 : 78.
Vayssière, 1885 : 54 ; 1935 : No. 20 (not paginated).
Vérany, 1853 : 390.

NOTE. Some specimens may be hybrids. Gwyn Jeffreys (1866) saw *Aplysia depilans* and *A. punctata* copulating in a tank in the Channel Islands. This may explain some of the intermediate forms, e.g. *A. lobiancoi* Mazzarelli, 1890 : 42.

Subgenus ***Neaplysia*** Cooper, 1863

Aplysia (Neaplysia) californica Cooper, 1863 : 57

Text-figs. 12 and 13

SYNONYMY : *A. ritteri* Cockerell, 1901–02 : 90.
? *A. nettiae* Winkler, 1959 : 8.[1]

DISTRIBUTION. West coast of North America : California and Lower California, including the Gulf of California.

MATERIAL EXAMINED. Several specimens from California (B.M. (N.H.)) and the Gulf of California, the latter sent by Dr. L. R. Winkler.

Pilsbry (1895, pl. 56) gave a figure of the whole animal. The external features and the shell were described by Cooper, who founded the subgenus on the peculiar flattening of the shell apex, which he regarded, probably incorrectly, as an " accessory plate ".

One of the giant members of the genus, attaining 375 mm. in length, 125 in breadth and 125 in height. Macginitie (1934) recorded a specimen weighing 5 lb. 12 oz.

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[1] Winkler's preserved specimens, described as a new species, are probably a variety. His account is not detailed enough to justify founding a new species on such slender grounds as open mantle tube, more frilly parapodia, and dark colouration, although the separation of the posterior attachments of the parapodia is a distinctive feature.

which laid 478 million eggs in 18 weeks. It is a plain species, with rather low, swollen body, thick in front, with the mantle and parapodia far back, the foot terminating in a long slender tail. It resembles *punctata* when it assumes the " sitting hare " position. The skin is soft, smooth and flabby. Colouring is very variable. Pale grey, green or dark brown, marbled with crimson or purple on the sides, and with a network of fine brown or black lines all over, usually with numerous large brown blotches and dark brown or black irregularly placed spots. Where these round spots lie on the intersections of the reticulations they may produce the illusion of a star pattern. The inner sides of the parapodial edges have a greenish background and bars of brownish black alternating with lighter areas, a common pattern in the genus. Mantle clear or with white flecks. Foot dark to black. All colour and markings may disappear with preservation.

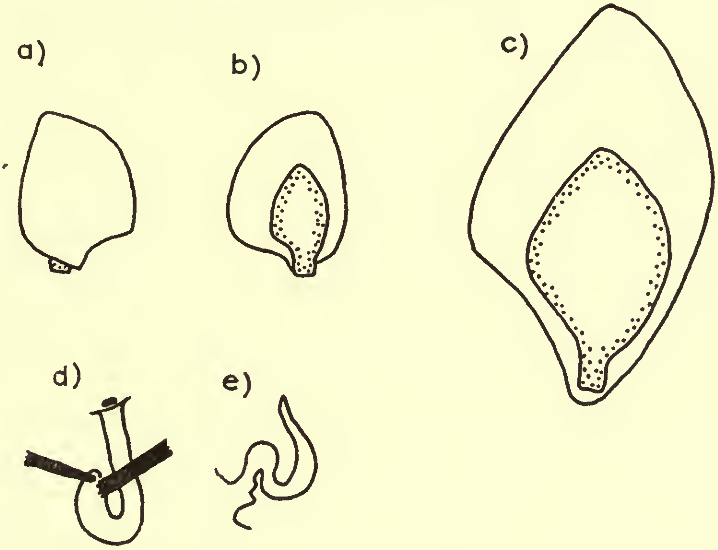

FIG. 12. *Aplysia californica.*

(*a*, *b*) Shell of one specimen in dorsal and lateral views. × $\frac{2}{3}$. Calcareous area dotted.

(*c*) Shell of a larger specimen, in which the calcareous and horny layers are distinct. It is evident that the " accessory plate " of Cooper (1863) is the flattened apical portion of the calcareous layer, which in (*a*) and (*b*) projects as a rectangular plate. × 2.

(*d*) Penis sheath in ventral view, with its two retractor muscles. × 1.

(*e*) Penis. × 2.

Head small but broad and clumsy, strongly contractile. Cephalic tentacles short, folded, lined with black and linked with the ventral sides of the mouth slit. Rhinophores close together, stout, black within the short slit ; when contracted they appear cup-shaped. Eyes small.

Foot moderate to broad, carunculate, rounded anteriorly, with defined wrinkled edges and a long slender tail. The animal attaches itself by the anterior and posterior ends of the foot, as many of its relatives do, raising the foot sole between these two points, but a sucker is not defined. Penis broad, tapering at the apex, coiled in the bulbous smooth-lined portion of the sheath (Text-fig. 12, *d*, *e*). Parapodia short, but can be raised high ; they arise close together, have slightly wavy, thin, freely mobile edges, and are joined posteriorly low down, forming a small platform over the foot.

Mantle small with a minute, usually closed tube, sometimes marked with concentric wrinkles. Anal siphon broad, thin, tubular, frilled on the edges and capable of considerable extension. A deep purple secretion from the mantle glands.

Mantle cavity widely open at both ends. Ctenidium small, unpigmented. Opaline gland large, compound, with one aperture, sometimes raised on a papilla. Genital aperture small, smooth, crescentic.

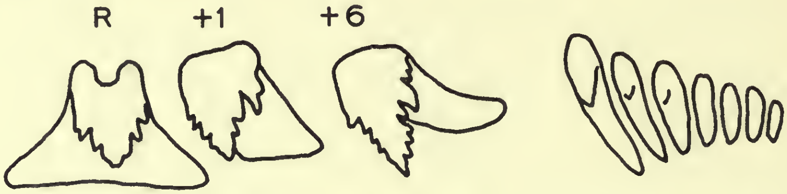

FIG. 13. *Aplysia californica.* Radular teeth. Rhachidian and first, sixth, and outermost laterals. × 80.

The shell (Text-fig. 12, *a–c*) is broad and short, rounded in shape, but narrowing almost to a point near the anterior edge. It is only slightly concave, without a spire and with very little calcareous matter. The growth lines are plainly visible and there are also radial striae. The anal sinus is weak. There is a recurved dorsal edge at the apex, and on the ventral side a rectangular plate, which Cooper described as an " accessory plate ". Examination of several recently preserved individuals, however, shows that this plate is the flattened calcareous portion of the apex, which separates from the horny apex. It is, therefore, a part of the shell, and not an accessory structure.[1]

The jaws consist of tall slender curved rods.

The radula in two small specimens had 50 rows and 56 rows and a formula of 32.1.32 and 40.1.40 respectively, but large specimens must exceed this considerably (Text-fig. 13). The rhachidian tooth has a broad basal plate, straight posteriorly, rounded at the corners, slightly waisted and with a narrow and deeply incised head. The cusp is shorter than the plate in mature teeth, a little longer in young teeth, with small irregular denticles, the basal one being short and divided. The first lateral has a rounded out-turned plate, broad rounded head and similar irregular denticulations. The slender cusp of the thirteenth tooth reaches the maximum length in the row, and the denticulations increase correspondingly, while the bases become more slender. There is a tendency for large denticles to become subdivided. The six outermost teeth are without cusps.

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[1] According to Winkler (1958), who examined young individals, the accessory plate "contains the built-in veliger and the metamorphic shell."

The caecum is very long, with enlarged recurved tip.

The cerebral ganglia form a broad flat band. The visceral ganglia are joined.

SPECIFIC CHARACTERS

Large Aplysias, with soft skin, irregularly mottled with brown and with fine reticulations. Shape clumsy, visceral region small, foot broad with long slender tail, parapodia short, mobile, joined low down posteriorly, mantle closed, with papilla, purple glands, broad flat shell with rectangular flattened calcareous apex and no spire, radula with elaborate but irregular denticulations, penis broad, tapering, opaline gland compound, uniporous.

California.

References (see also synonyms)

Cockerell, 1915 : 84.
Cooper, 1867 : 14.
Lowe, 1934 : 43.
Macginitie, 1934 : 300.
Parker, 1918 : 139.
Pilsbry, 1895 : 89, pl. 56, as *Tethys.*
Winkler 1958 : 348; 1959 : 8.

Subgenus ***Varria*** nov.

Aplysia (Varria) brasiliana Rang, 1828 : 55, pl. 8

Text-figs. 14 and 15

SYNONYMY : *Tethys floridensis* Pilsbry, 1895 : 82. I have seen the type, and could find no significant difference in structure between it and Rang's species.

A. livida d'Orbigny, 1837 : 206. Mis-spelt *lurida* on plate 18.

A. guadeloupensis Sowerby, 1869 : pl. 5, named from the shell only, may be this species.

A. cailleti Deshayes, 1857 : 140, probably this species.

DISTRIBUTION. The species belongs to the Atlantic Ocean, and ranges from New Jersey in the north to St. Helena in the south. It has been found in Florida, Texas, the West Indies and Brazil, and on the coast of Ghana in West Africa.

MATERIAL EXAMINED. Numerous examples from the eastern seaboard of North and South America and from West Africa.

Rang figured *brasiliana* and his figure was copied by Pilsbry. Marcus (1955) has published an excellent account of it and has studied the development. He can find no valid distinction between *brasiliana* and d'Orbigny's *livida.* I am indebted to Dr. Marcus for observations on the living animal and for co-operation in preparing the following account.

Medium to large Aplysias, high and massive, with elongated head and neck, but strongly contractile. Much swollen posteriorly. Reaching 270 mm. when alive, and from 140 to 170 mm. high. Skin smooth, but rugose when preserved, " like peccary leather ". Colour usually yellow, deep brown, bottle green, grey or purplish black, unicoloured or spotted yellow, dark brown or green, with black pigment forming a fine veining or network. There may be white or dark spots or chalky granules, connected by a network. Occasionally creamy white specimens occur. A very variable species. The parapodia are blotched with black on their inner surfaces, with alternately dark and light areas arranged vertically near the edges, which are light. Foot dark brown to light brown, usually uniformly coloured.

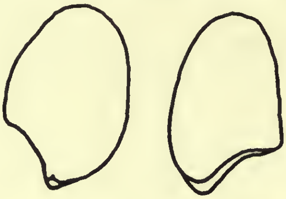

FIG. 14. *Aplysia brasiliana.* Shell of two specimens in ventral and dorsal views respectively. × $\frac{2}{3}$.

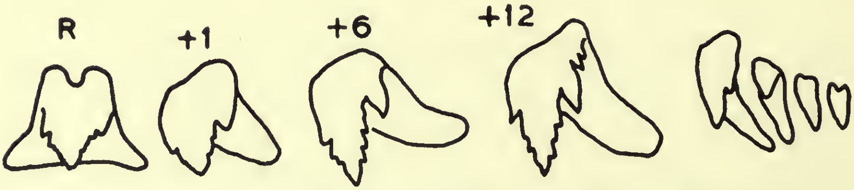

FIG. 15. *Aplysia brasiliana.* Radular teeth. Rhachidian and first, sixth, 12th and outermost lateral teeth. × 80.

Mantle dark with radiate or irregular light areas. Ctenidium usually pigmented. Tips of the cephalic tentacles and rhinophores light.

Head and neck elongated, small. Cephalic tentacles broad, but not meeting mid-dorsally. Eyes in clear patches. Rhinophores small, conical, set close together, slit half-way down.

Foot narrow to medium, with a short tail. Penis long, broader at the base, tapering but not filiform, penis sheath smooth. Parapodia large, can be widely opened exposing the whole of the dorsal area, joined posteriorly very far back and low down on the root of the tail, the edges upstanding before joining. (Rang's figure is misleading.) The edges are thin and wavy, but not fimbriated.

Mantle large, set far back, thin. Mantle aperture minute, on the tip of a papilla. Anal siphon of moderate to large size, plain or wavy, sometimes projecting backwards, wide but not high. Mantle glands secrete a magenta red secretion.

Mantle cavity open at both ends. Ctenidium large, but contractile. Opaline gland compound, uniporous. Marcus says that the secretion is greenish yellow but not fetid. Genital aperture smooth or furrowed, pigmented, set well under cover of the mantle. Genital groove plain.

Shell (Text-fig. 14) narrow to broad in large animals, concave, dark yellow, with the apex hard and hooked, but without spire. Anal sinus shallow, firm edged, dorsal part of apex recurved. Usually with marked concentric rings and one or more radial striae.

Jaws very dark. Rods long, slender, almost straight, but some may have bent tips with fringed edges.

Radula almost as broad as long, 65–70 rows, formula 43.1.43 (Text-fig. 15). Rhachidian tooth narrow, with long plate and narrow head, simple cusp bearing one basal denticle on each side and a few irregular ones. First lateral small, with rectangular plate and similar denticulations. Remaining teeth with longer, narrower cusps, a pair of lateral denticles, and the other denticles so small that the edge appears beaded, except in young teeth. Further along the row the plates become attenuated and the cusps longer. About three terminal teeth are degenerate.

Caecum appears on the surface and is straight and inflated at the tip.

Cerebral ganglia band-like, fused. Visceral ganglia joined.

SPECIFIC CHARACTERS

Large bulky body, self-coloured or spotted. Simple cephalic tentacles, slender rhinophores set close together, long neck, narrow foot, long tapering penis, very large parapodia joined low down posteriorly, mantle aperture tubular, opaline gland compound, uniporous, simple radula with high narrow rhachidian tooth. Young specimens may have a hole in the mantle.

West Atlantic from New Jersey to Brazil; East Atlantic: Ghana and Saint Helena.

References (*see also synonyms*)

Adams & Adams, 1858 : 35 (as *Syphonota lurida*).
Marcus, 1955 : 4.
Pilsbry, 1895 : 82 and 79 (*livida*), as *Tethys*.
Pruvot-Fol, 1934 : 38.

Aplysia (Varria) cervina Dall & Simpson, 1901 : 365, pl. 56, fig. 2

Text-figs. 16 and 17

SYNONYMY : *pilsbryi* Letson, 1889 : 193. Yucatan.

DISTRIBUTION. Atlantic seaboard from Eastern U.S.A., through Central America and the West Indies to Brazil.

MATERIAL EXAMINED. Numerous specimens from eastern U.S.A. and Central America, including two '*A. pilsbryi*,' belonging to the Academy of Natural Sciences, Philadelphia.[1]

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[1] Except for an upturned edge to the rim of the mantle where the purple gland lies, to which Letson referred, there is no structural difference between these specimens and *cervina*.

The species was named by Dall & Simpson from nine rather small specimens from Porto Rico. MacFarland (1909 : 38) gave a long account of its anatomy.

Of moderate size, smaller, more bulky and plainer than *brasiliana*, reaching about 70 mm. when preserved, but more elongated when alive (Text-fig. 16*a*). Soft, plump and smooth, flabby. Grey with scattered round black or smoky brown spots and flecks up to 2·5 mm. in diameter, with reticulations and blotches between the spots, and there may be lighter areas. A specimen may have about 30 spots on the side of the body (Text-fig. 16*b*). Mantle dappled with alternating light and dark patches, sometimes arranged radially. Inner sides of the parapodia grey to black,

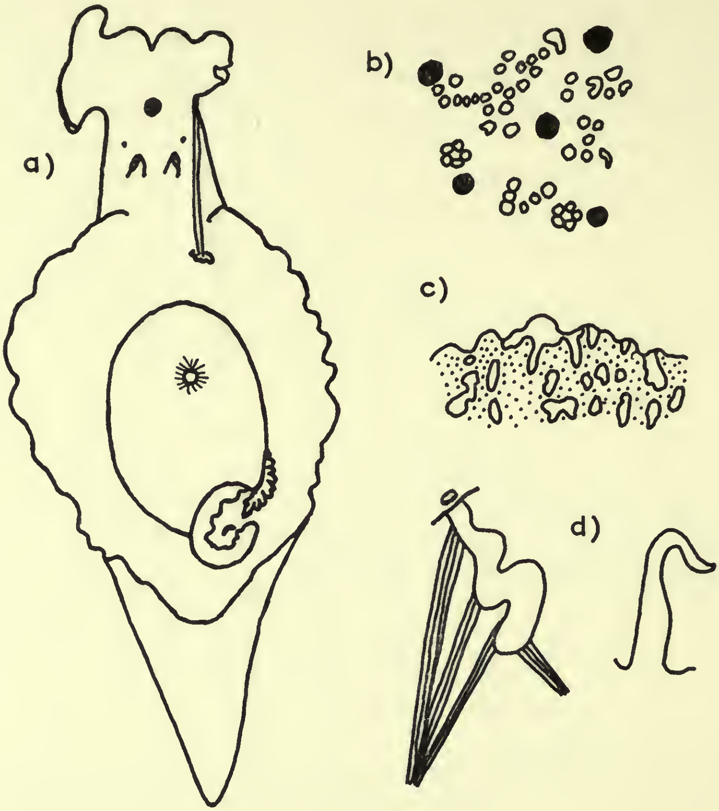

FIG. 16. *Aplysia cervina.*

(*a*) Dorsal view of a specimen from Anguilla, West Indies. × $\frac{2}{3}$.
(*b*) Pattern on the side of the body, composed of round dark brown spots and clear areas, sometimes in clusters or rosettes on a light brown background, which is finely reticulated, but the reticulations have not been figured.
(*c*) Pattern on the inner side of a parapodium, made up of dark and light blotches.
(*d*) Penis sheath and penis. × $1\frac{1}{2}$.

with vertical black and light areas, but clear on the edges (Text-fig. 16*c*). Foot dark. All colour and markings may disappear after long preservation.

Head and neck rather small. Cephalic tentacles plain, short in contracted specimens, but can be spread like elephant's ears. Rhinophores conical, fairly widely spaced, but not as wide as the parapodial origins, deeply slit. Eyes far apart.

Foot with narrow to medium sole, tough and wrinkled in contraction, the anterior border with rounded angles, the tail short, triangular or blunt. Penis (Text-fig. 16*d*) short, broad, flattened, capable of great elongation, may be curled laterally and longitudinally, apex acute. Sheath small, with large muscles attached by two strong bands to the bulbous portion, the lining of which is smooth. Parapodia rather thick, not large, about three-quarters of the length of the animal, the anterior ends widely separated, edges slightly sinuous, coming close together and joined low down posteriorly, forming a flat extension of the mantle floor.

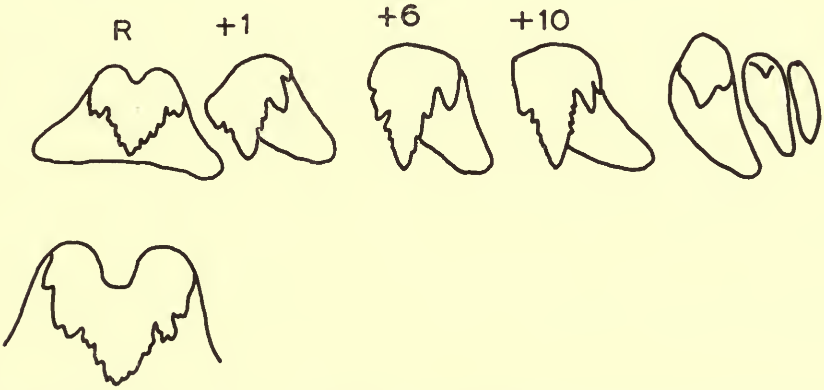

FIG. 17. *Aplysia cervina.* Radular teeth. Rhachidian, first, sixth, tenth and outermost laterals. × 80. Below, the cusp of an old rhachidian tooth, enlarged, to show irregularity of the denticulation.

Mantle thin, with a small aperture on a papilla, sometimes with radiating lines around it. Siphon broad, fimbriated, not high. Purple glands present.

Mantle cavity "roomy" (MacFarland), opening out behind between the low fused parapodia. Ctenidium large. Opaline gland compound with a single aperture on a low thickened elevation. Genital aperture oblique, pigmented, the edge sometimes projecting in a small peak dorsally. Genital groove deep and conspicuous.

Shell thin, flat, narrow to broad and rounded. Apex recurved dorsally but imperfect ventrally. Anal sinus long and shallow. Calcareous and horny parts present.

Jaws with rounded edges.

Radula 38–48 rows, formula 22.1.22 but an older specimen may have up to 40 teeth on each side (Text-fig. 17). Rhachidian with broad plate, slightly excavated on the posterior border and more deeply so anteriorly, between the two a narrow or waisted effect. Cusp longer than the plate, but shortening with wear. Two pairs of lateral denticles near the base larger than the others, which are small and regular, but not deeply cut, becoming irregular with age. First lateral with bulbous head, higher on the antero-lateral portion, the remainder of the plate tapering, out-turned. In the remaining laterals the cusp does not lengthen greatly, the plate remaining bulbous anteriorly and the denticles exhibiting a common type, the large basal denticle sometimes splitting or even becoming multidenticulate. The last four or five teeth in the row are rounded and weak.

Caecum curved, lying flat on the surface where exposed.

Cerebral ganglia completely fused. Visceral ganglia joined but their double origin can be seen anteriorly.

SPECIFIC CHARACTERS

Moderate size, plain unfimbriated aspect, with scattered brown spots on the sides of the body, vertical bands of dark and light on the inner sides of the parapodia, small head and plain cephalic tentacles, short broad flattened penis, narrow foot, low joined parapodia, small open papilla on the mantle, compound uniporous opaline gland, constricted plate of the rhachidian tooth and bulbous heads of the laterals.

West Atlantic from U.S.A. to Brazil.

References (*see also synonymy*)

Engel, 1936 : 13.
van Jhering, 1915 : 135, 140.
MacFarland, 1909 : 38.
Marcus, 1959 : 3.

NOTE. Van Jhering thought that MacFarland confused *brasiliana* and *cervina* and that the latter belongs to the West Indies, but his distinction refers to colour and markings only. Although there are resemblances the species appear to be distinct.

Aplysia (Varria) cornigera Sowerby, 1869 : pl. 9

Text-fig. 18, *a*, *b*, *c*

DISTRIBUTION : India, Ceylon, Indo-China, the Philippines.

MATERIAL EXAMINED. Several specimens from India, Ceylon and the Philippines.

The species was named from a shell only by Sowerby. Farran (1905) stated that it is a common Ceylon species. A description was given by the author (1944 : 2).

Aplysias of moderate size, usually about 90 mm. long, 66 mm. wide and 75 mm. high when preserved, rather bulky. Brownish olive with clear spaces, in the centre of which there may be a black spot. Mottled pigment on the inner sides of the parapodia near the edges. All pigment may disappear with long preservation. Skin very smooth and not strongly contractile.

Head and neck broad and short. Cephalic tentacles flat, leaf-like, wholly lateral and slightly rolled at the edges, continued over the mouth. Eyes small, distinct. Rhinophores slender, rounded, set well back, close together.

Foot narrow, defined laterally, with long pointed tail. Penis (Text-fig. 18*c*) short, flat, sickle-shaped, moderately broad at the base, the spermatic groove lying along its edge. Parapodia arising about half-way between the rhinophores and the genital aperture, united low down posteriorly but above the level of the mantle cavity floor, so that there is a shallow mantle cavity pocket. Margins smooth or slightly sinuous but not frilled. Dorsal slit wide open.

Mantle of moderate size. Mantle foramen minute or closed, with radial markings around it. Purple glands present. Anal siphon short and broad.

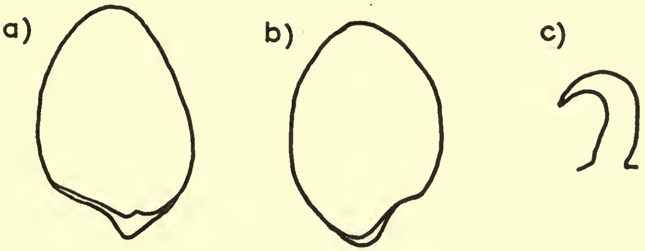

FIG. 18. *Aplysia cornigera.*

(*a*) Ventral, (*b*) dorsal view of the shell. × $\frac{2}{3}$.
(*c*) Penis. × 2.

Mantle cavity floor almost flat, with a small pocket behind. Genital aperture smooth, crescentic, pigmented. Even in small specimens the genital duct shows plainly through the floor. Opaline gland simple, multiporous, though there is a tendency for several gland cells to join and open together in the anterior part of the gland.

Shell (Text-fig. 18, *a*, *b*) thin, delicate, broadly ovate, rounded anteriorly, deeply concave. Apex inturned but weak. Anal sinus short and not deep. A specimen 90 mm. long had a shell measuring 43 × 36 mm.

Jaw rods short and compact, very dark, curved.

Radula about 40 rows, formula 30.1.30. The rhachidian tooth has a broad triangular basal plate, short cusp with small blunt denticles, the two basal ones larger than the others. The laterals have denticulate main cusps, with one larger denticle mesially and a group of very irregular denticles laterally, the penultimate denticle being the largest, the outermost three to five teeth are vestigial.

The exposed portion of the caecum lies flat on the surface of the digestive gland.

The visceral ganglia are partly fused, the cerebral entirely so.

The species has been compared by Farran (1905) with *A. pulmonica* Gould from Samoa. It is quite distinct, however, and differs from that species in its shape, narrow foot, multiporous opaline gland, shape of the shell, radular formula and tooth pattern.

SPECIFIC CHARACTERS

Moderate size, smooth, mottled and spotted skin, narrow foot and tail, low fusion of the parapodia posteriorly with shallow mantle cavity pocket, closed or almost closed mantle, simple opaline gland with many apertures, broadly ovate delicate shell and denticulate radular teeth.

Northern part of Indian Ocean and East Indies.

References

Eales, 1944 : 2.
Farran, 1905 : 2.
Pilsbry, 1895 : 103, as *Tethys*.

Aplysia (Varria) cronullae sp. nov.

Text-figs. 19 and 20

DISTRIBUTION. Australia : New South Wales.

MATERIAL EXAMINED. Three specimens from Cabbage Tree Creek, Cronulla, collected at low water in 1951 by Dr. H. Lemche, and one specimen, juvenile, from Port Hacking, collected in 1914 by Dr. Th. Mortensen. The largest specimen in the University Museum, Copenhagen, is designated as the holotype. One of the others was presented to the British Museum (Nat. Hist.) by Dr. Lemche.

Of medium size, but massive and bulky. Alive, Dr. Lemche states that it measured 110–140 mm. in length, 40–50 mm. wide and high, the head 25 mm. long and 20 mm. broad. The largest preserved specimen measures 106 mm. long, 43 mm. wide and 58 mm. high, the foot being 27 mm. wide (Text-fig. 19, *a*, *d*). Colour greyish green, mottled dark brownish green. In addition to the irregular blotches there are fine black lines forming a network or running parallel, especially on the head. The inner sides of the parapodia have dark blotches, but the edges are light. The mantle has radiating stripes of pigment from the central papilla to the edges. Foot mottled. The colour is very variable and may be supplemented by white patches. Skin soft.

Head rather large, neck short and wide. Cephalic tentacles standing out well on the sides of the head with the folded part small, then becoming sinuous, with wide rounded mouth flaps. Rhinophores round, elongated, pointed, close together, slit half-way, the lining of the slit dark. Eyes very small.

Foot of medium width, soft, the edges defined, the anterior edge rounded, with a dark line on the border, tail short and pointed. Penis sheath small, straight, with two small retractor muscles. Penis (Text-fig. 19*f*) narrow, unpigmented, filiform.

Parapodia well developed, soft, thin-edged but sinuous, rounded, arising about as far back from the rhinophores as these are from the cephalic tentacles, meeting but not joining low down on the tail, forming a platform continuous with the mantle cavity floor.

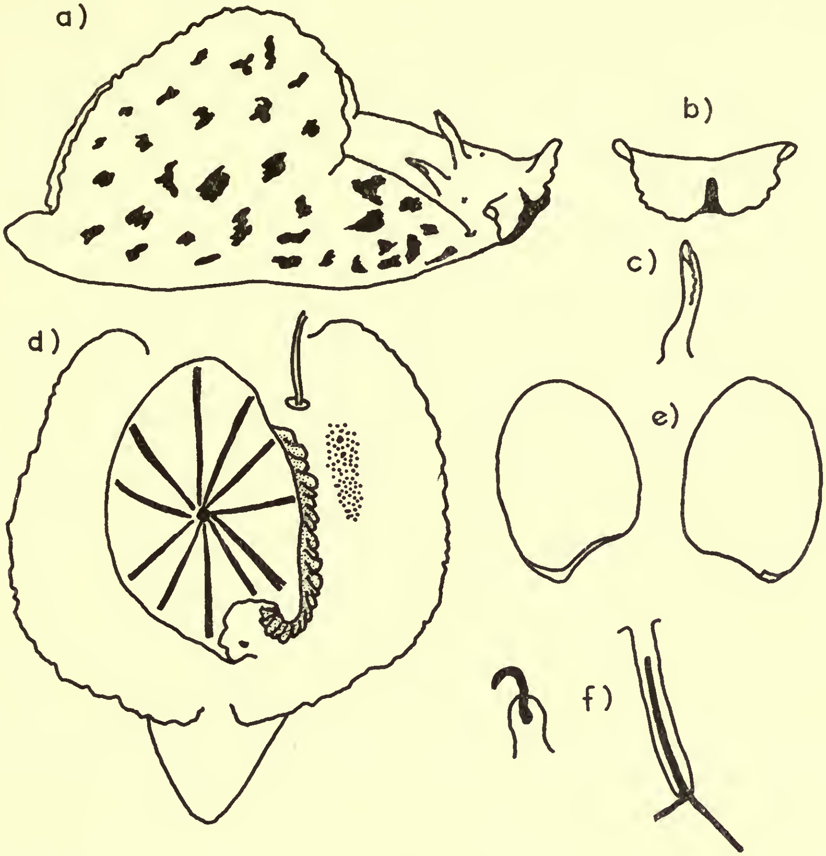

FIG. 19. *Aplysia cronullae.*

(*a*) Lateral view, showing the blotched skin, but not the lines or reticulations. × $\frac{2}{3}$.
(*b*) Anterior view of the cephalic tentacles and mouth slit. × 1.
(*c*) A rhinophore.
(*d*) Dorsal view of the mantle to show the bands of pigment readiating from the central papilla. The ctenidium, genital aperture and sperm groove, anal siphon, anus, opaline gland apertures, parapodia and tail are figured. × 1.
(*e*) Shell in dorsal and ventral views. × $\frac{2}{3}$.
(*f*) Penis partly protruded, and right, in its sheath, with the two retractor muscles. The penis is unpigmented, but has been drawn in black, owing to its small size. × $1\frac{1}{2}$.

Mantle (Text-fig. 19*d*) thin with a small open aperture on a minute papilla. Anal siphon well developed, broad and short, fluted. Purple glands dark.

Mantle cavity large, genital aperture pigmented, smooth-edged, the duct lying straight under the mantle cavity floor. Opaline gland large, more than twice the size of that in *A. sydneyensis*, simple, multiporous, curved, pyriform.

Shell (Text-fig. 19*e*) 38 × 27 mm., almost flat, with well marked concentric ridges, weak apex and slight anal sinus.

Jaws pale, rectangular, the rods of moderate length, straight or slightly curved.

Radula (Text-fig. 20) large, with about 50 rows and a formula of 28.1.28. Rhachidian tooth with wide basal plate, almost straight posteriorly, deeply incised anteriorly. Cusp short, rounded, with a few irregular denticles. First lateral with triangular basal plate and firm denticulations. Along the row the plates lengthen, then broaden considerably, becoming squared off. The denticulations are strong but not regular, the cusps of moderate length only. Three teeth are vestigial at each end of a row.

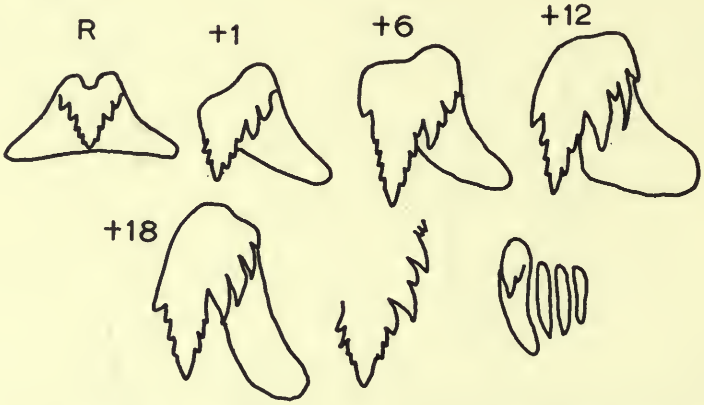

FIG. 20. *Aplysia cronullae*. Teeth from the radula. Rhachidian, first, sixth, 12th, 18th and four outermost laterals. × 80. A small portion of the blade of a lateral near the middle of the row has been enlarged.

The caecum lies flat on the surface of the digestive gland and may be inflated at the tip.

Nerve ganglia : Cerebral ganglia fused, visceral also.

SPECIFIC CHARACTERS

Medium size, bulky shape, greenish colour with dark brownish green irregular blotches, fine black reticulations and parallel lines on the head, the inner sides of the parapodia with blotches, but the edges light, mantle with radiating bands of dark pigment from the central papilla, sometimes white patches. Skin soft. Cephalic tentacles large, rounded, rhinophores slender, set close together. Foot of medium width, defined edges and pointed tail. Penis sheath small, penis filiform. Parapodia rounded, meeting low down posteriorly. Mantle with a small aperture on a papilla, anal siphon broad and short, purple glands. Opaline gland large, simple, multiporous. Shell broad, flat, with weak apex and shallow sinus. Radula about 50 × 28.1.28, with irregular denticles. Caecum straight.

Australia, New South Wales.

Aplysia (Varria) dactylomela Rang, 1828 : 56, pl. 12

Frontispiece and Text-figs. 1–8

SYNONYMY : *A. d.* var. *aequorea* Heilprin, 1888 : 326.
angasi Sowerby, 1869 : pl. 8 ; Hedley, 1918 : 107 ; 1923 : 314, pl. 33.
annulifera Thiele, 1930 : 586.
argus Rüppell & Leuckart, 1828 : 23.
benedicti Eliot, 1899 : 513.
fimbriata Adams & Reeve, 1850 : 63.
lobata? Bergh, 1908 : 148 (?juvenile). See also *parvula*.
megaptera Verrill, 1899 : 545 ; 1901 : 26.
var. *ocellata* d'Orbigny, 1835–44 : 44, pl. 5 (*non* Adams, 1861).
odorata Risbec, 1928 : 51 and 1951 : 123 var. *bouraili*.
operta Burne, 1906 : 51. ?Mis-spelt *aperta* (as *Tethys*) by Turton 1932.
panamensis Pilsbry, 1895 : 88, as *Tethys*.
protea Rang, 1828 : 56.
radiata Ehrenberg, 1831 (pages not numbered) (*non* Crouch, 1826).
schrammii Deshayes, 1857 : 140.
scutellata Ehrenberg, 1831.
tigrina Rang, 1828 : 57 (*non* Q. & G.).
velifer Bergh, 1905 : 12 (juvenile).
Syphonota viridescens Pease, 1868 : 77.
?*Syphonota keraudreni* ; Angas, 1867 : 227 ; Sowerby, 1869 (*non* Rang).
guadeloupensis Sowerby, 1869 : pl. 5 may be *dactylomela* or *brasiliana*.

Specimens recently collected and known locally as *A. grandis* (Pease, 1860) were sent to me by Dr. Alison Kay, of the University of Honolulu. They proved to be *dactylomela*. The identity of Pease's *Syphonota grandis* remains in doubt.

DISTRIBUTION. Worldwide in warm seas. Recorded from Bermuda, Florida, Mexico, the West Indies, Panama, Brazil, the Canaries, Cape Verde Islands, Ghana, the Red Sea, Ceylon and India, Mauritius, South Africa, China, Japan, the East Indies, the Philippines, Samoa, Tonga, the Gilbert Islands, Australia and New Zealand.

MATERIAL EXAMINED. Numerous specimens from all areas in its range.

No species of *Aplysia* has received more notice than this, owing, no doubt, to its large size, wide distribution and striking appearance. Rang, who named it, gave a poor figure of it, and recognized *protea* and *tigrina* as separate species, although they are almost certainly the same. The types cannot be found. The species varies very little in different parts of the world. It has received local names ; Engel (1929) correlated these and showed that *dactylomela* is circumtropical. A beautiful coloured figure, based on a painting by Dr. J. Stuart, was published by Hedley in 1923, and has been used for a black and white illustration as frontispiece to this Memoir. Baba (1949) also figured it in colour. MacFarland (1909 : 14) gave a lengthy account of its structure.

Large, plump and bulky, attaining more than 400 mm. in length when alive, though many specimens do not exceed 300 mm. and the largest contract to this length when preserved (Text-fig. 1). Contracts to the sitting hare position, the head and neck being drawn back almost to the anterior edges of the parapodia. In extension these regions are long and rather flattened. Skin soft, but may become rough and tough in contraction. Ground colour dark brown to olive green or yellowish green, with light bluish eye flecks surrounded by large, scattered, black or brown rings of irregular sizes and badly defined outlines (Text-fig. 2). There are usually from 20 to 30 rings on each side of the body, and there may be one on the centre of the head. The rings may reach 25 mm. in diameter and 3 mm. in thickness. Sometimes there are pigment bands between the rhinophores and the cephalic tentacles, and there is usually a dark blotch on the dorsal surface of the tail. The rings may be prolonged on their outer edges into branched black lines which may become reticulate and anastomose with those from adjacent rings. From a study of young specimens it is evident that the rings are formed from the fusion of strands of pigment, hence the inter-annular connections. The centre of the ring may be traversed by similar pigment strands. White opaque dots, probably of a calcareous nature, and finer black anastomosing lines may also be present. On the inner sides of the parapodia the black pigment is massed in the form of branched vertical bands ; the edges are light. There is a tendency for the contracted tentacles, parapodial edges and anal siphon to assume a frilled appearance, accentuated by their sinuous or fluted margins. The var. *fimbriata*, common in the Indian Ocean, exhibits this character. The foot sole is pale with dark brown irregular blotches. The animal is a strong swimmer.

Head and neck large, but short and squat in contraction. Cephalic tentacles large, with smooth or fringed margins, folded as usual, continued to the sides of the mouth. Rhinophores thick, set close together, with shallow grooves notched on one side, when contracted appear cup-shaped.

Foot (Text-fig. 3*a*) broad, thick, soft, but becomes hard in contraction, its edges well defined, front edges rounded, tail short and blunt. Penis sheath attached by two strong retractor muscles, supplemented by finer strands at the sides (Text-fig. 5*c*). Penis white, broad, spatulate, long when extended, the sperm groove winding spirally round it. Parapodia (Text-fig. 4) large, powerful, natatory ; they commence close together ; edges sinuous or fluted, occasionally smooth, not normally covering the anal siphon, joined posteriorly low down on the tail, forming a platform-like extension of the mantle cavity floor or at most a low pocket. Sometimes they are free, with a pigmented gap between the lobes.

Mantle (Text-fig. 4) large, thin, sometimes rough, with a small foramen, but more commonly a closed conical papilla. Anal siphon large and frilled. Deep purple mantle gland exudate. *A. protea* of Martinique, according to d'Orbigny (1853), is called locally " Baril de vin " owing to the deep reddish purple secretion it exudes when disturbed.

Mantle cavity shallow, ctenidium of moderate size, usually not pigmented. Opaline gland (Text-fig. 5*a*) compound, forming a large solid trihedral block hanging beneath the mantle cavity floor by its duct. Genital aperture smooth, oblique, crescentic or with a little triangular peak; marked by a black streak.

Shell (Text-fig. 6) large, broad, rounded, with an oblique apex, strongly calcified, with hardly any trace of a spire, but with a deeply excavated anal sinus. It varies with age from thin and delicate to thick and solid. Postero-dorsal edge recurved.

Jaws (Text-fig. 7, *e*, *f*) rectangular, about 5 × 3 mm., dark in colour. Jaw rods short, curved, broadening at their free ends, or straight and truncated.

Radula (Text-fig. 7, *a–d*) large. For a specimen measuring 170 mm. Macnae gave the formula 73 × 67.1.67. Rhachidian tooth wide, with slightly excavated basal plate and deeply incised head, short, finely denticulate cusp and one pair of larger denticles. Laterals with broad heads and strong denticulate cusps, with two or more side denticles, and tapering, out-turned basal plates. The cusp lengthens as the distance from the rhachidian tooth increases, and becomes long, straight and spiky, losing its denticles except for a stout one laterally. The pattern is of a series of long straight cusps, each row overlapping the succeeding row. The four outermost teeth are degenerate.

Caecum (Text-fig. 8*b*) large, lying flat on the surface of the digestive gland where exposed.

Cerebral ganglia (Text-fig. 8*a*) fused, but may show their double origin. Visceral ganglia also fused.

SPECIFIC CHARACTERS

Large bulky Aplysias, of basic yellowish green colour, with numerous large black rings of irregular sizes on the sides of the body, thick rhinophores with short notched apices, broad foot with blunt tail, frilled swimming lobes joined low down posteriorly, broad spatulate spirally grooved penis, compound uniporous opaline gland, purple secretion, lateral teeth of the radula with long straight smooth cusps.

Circumtropical.

References (*see also synonyms*)

Allan, 1932 : 420, as *angasi* ; 1950 : 212.
Angas, 1867 : 228, as *tigrina* : 1877 : 190, as *angasi*.
Arango, 1878 : 155, as *protea*.
Baba, 1936 : 7 and 1949 : 124.
Bergh, 1905 : 6, as *benedicti*.
Dakin, Bennett & Pope, 1953 : 264, as *angasi*.
Dall & Simpson, 1902 : 365, as *T. protea*.
Dobson, 1880 : 159.
Eales, 1944 : 3, as *fimbriata* ; 1957 : 179.

Engel, 1927 : 84 ; 1929 : 147 ; 1936 : 5.
Gould, 1852 : 210, as *fimbriata*.
Hedley, 1910 : 370, as *Tethys tigrina*.
MacFarland, 1909 : 14, as *Tethys*.
Macnae, 1955 : 226 ; 1957 : 289.
Marcus E. & E., 1955 : 14.
Martens, 1880 : 307, as *tigrina* ; 1894 : 93.
Mörch, 1862 : 23, as *protea* ; 1875 : 176.
Odhner, 1932 : 27.
Olmsted, 1917 : 225.
d'Orbigny, 1854 : 117, as *protea*.
Pruvot-Fol, 1933 : 104 ; 1934 : 38 ; 1947 : 111 ; 1953 : 33.
Quoy & Gaimard, 1832 : 311.
Rochebrune, 1881 : 264.
Taki, 1932 : 212, as *Tethys*.
Thiele, 1910 : 123, as *Tethys*.
Winckworth, 1927 : 95, as *benedicti*.

Aplysia (Varria) denisoni Smith, 1884 : 89

Text-fig. 21

DISTRIBUTION. Indian Ocean (Cocos Keeling Islands), West Australia (Abrolhos Islands) ; South Pacific, Queensland and New South Wales.

MATERIAL EXAMINED. Specimens from Cocos Keeling Island and Eastern Australia.

The species was described by E. A. Smith from Queensland. Later O'Donoghue (1924 : 531) recorded and described it from the Abrolhos Islands off West Australia.

Aplysias of moderate size, up to 150 mm. long, 32 mm. broad and 61 mm. high when preserved (Text-fig. 21*a*). Olive green, with dark mottlings and black veining. Inner sides of parapodia with vertical black and brown bands. No pigment on the foot, mantle roof and ctenidium, but this may have faded, and all trace of colour may disappear with long continued preservation. Skin soft, but not flabby, smooth.

Head and neck large, broad and rather flat. Cephalic tentacles very wide, flat and plate-like, only slightly rolled on the edges (Text-fig. 21*b*). Eyes rather large. Rhinophores small, close together.

Foot large, muscular but not tough, edges not well defined, tail short, pointed. Penis short, broad and spatulate. Parapodia small, low, commence far back, rounded, edges irregular but not fimbriated, joined low down on the foot, making a platform or low wall behind the visceral mass. Dorsal slit wide open.

Mantle thin, weak, not large, with small conical papilla at the point of closure of the shell covering. Purple glands present. Anal siphon large, broad, jagged.

Mantle cavity widely open, exposing the large ctenidium. Opaline gland compound, uniporous. Genital aperture plain, smooth, crescentic, the duct not inflated beneath the mantle cavity floor, genital groove weak.

Shell (Text-fig. 21*c*) ovate, broad, firm, with flat calcified apex, which is oblique. Anal sinus long and moderately deep. About ten rays spread from the apex to the anterior margin.

Buccal mass small. Jaws narrow, rods very long, slender, slightly curved at the apex, loosely arranged.

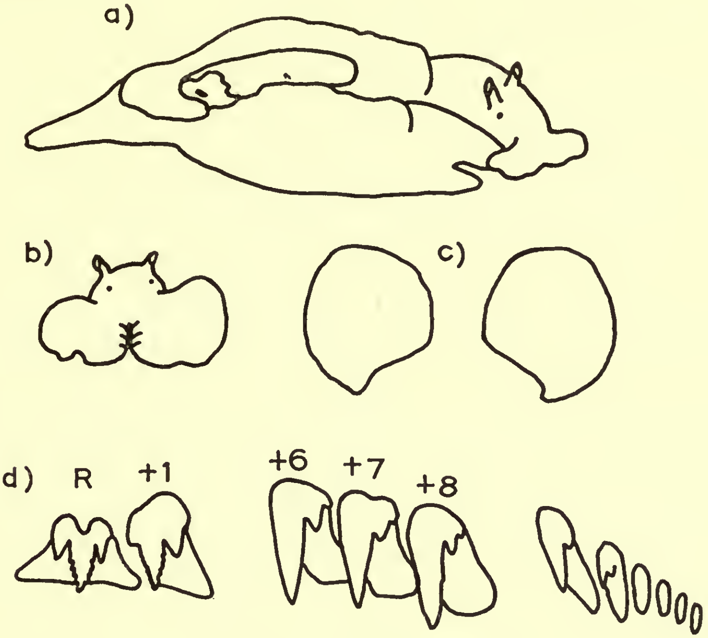

FIG. 21. *Aplysia denisoni*.

(*a*) Lateral view of a specimen from Australia. × 1.
(*b*) Head to show the large, plate-like cephalic tentacles.
(*c*) Shell in dorsal and ventral views. × $\frac{2}{3}$.
(*d*) Radular teeth. Rhachidian, first, sixth, seventh, eighth and outermost lateral teeth. × 80.

Radula (Text-fig. 21*d*) broad, 8·5 × 9 mm. in 83 mm. specimen. Formula 70 × 53.1.53. Rhachidian with broad flat basal plate, paler than the laterals, cusp with faint denticulations and one pair of large denticles. First lateral with short, almost rectangular basal plate, weakly denticulate cusp and a large lateral basal denticle. The main cusp lengthens considerably as distance from the centre increases, but the laterals remain simple, with smooth or feebly denticulate cusps and large basal denticles. Older teeth become quite smooth. Up to five vestigial teeth at the end of the row.

Caecum small, appearing flat on the surface of the digestive gland.

Cerebral ganglia fused as a flat band. Visceral ganglia joined but recognizably paired.

Specific Characters

Moderate size, very large plate-like cephalic tentacles, rounded parapodia joined low down on the foot posteriorly, minute mantle papilla, compound uniporous opaline gland, ovate calcified shell with narrow oblique apex and long anal sinus, broad radula with weak denticulations and elongated cusps to the laterals.

Australia and southern Indian Ocean.

References

Hedley, 1909 : 370.
Pilsbry, 1895 : 102, as *Tethys*.

Aplysia (Varria) extraordinaria Allan, 1932 : 314

Text-figs. 22 and 23

Distribution. South Pacific, from Hawaiian Islands to New South Wales, Australia.

Material examined. The type specimen from the Australian Museum, Sydney, taken by Miss Allan at Port Hacking, New South Wales, two specimens brought to this country for the International Fisheries Exhibition in 1883 from Port Jackson, now in the British Museum (Natural History), and one specimen from the Paris National Museum, collected by M. Ballieu in the Hawaiian Islands in 1874.

A well defined species, large (at least 300 mm. long when alive), slender and active. It shrinks to about half this length when preserved, and while remaining soft and flabby may become intensely wrinkled. The type specimen (Text-fig. 22) measures 146 mm. long, 32 mm. wide and 73 mm. high. The colour is deep umber brown with reticulate black veining and scattered black or brown blotches. There may also be light spots and vertical white bands, and black spots on the head. The inner sides of the parapodia have vertical bands of light and dark near the edges, but oval light areas on a black background below. The mantle is mottled brown and white, with concentric lines of brown pigment along the edges. All pigment may bleach as the result of long continued preservation.

Head small, long and narrow, with slender neck (Text-fig. 23*a*). Cephalic tentacles wide, continued as broad rounded side flaps to the mouth. Eyes small. Rhinophores acutely pointed, slender, very close together, set far back and slit more than half-way.

Foot very long and narrow, only 22–26 mm. wide in the type, soft and not thick. Anterior border rounded and slightly enlarged, edges not well defined laterally, tail long and slender. Traces of pigment remain. Penis sheath small, penis elongated, stout at the base, pointed, with straight sperm groove to the tip (Text-fig. 23*c*). Parapodia large, rounded, arising close together and meeting low down posteriorly, forming a 24 mm. extension of the mantle cavity floor. In another specimen they appear to be free. Edges sinuous or smooth. Mobile and probably natatory.

Mantle small, 55 × 30 mm., thin, with little overhang anteriorly, but a wide flap laterally. Foramen small, with contraction rings around it. Anal siphon 19 × 16 mm. wide, tall, thin and leaf-like. Mantle glands well developed, spotted with dark pigment, so probably purple is secreted.

Mantle cavity open at both ends. Ctenidium large, 30 × 15 mm. Opaline gland small, simple, multiporous. Genital aperture not pronounced, plain edged. Genital groove slight, marked by cross stripes of brown in the type.

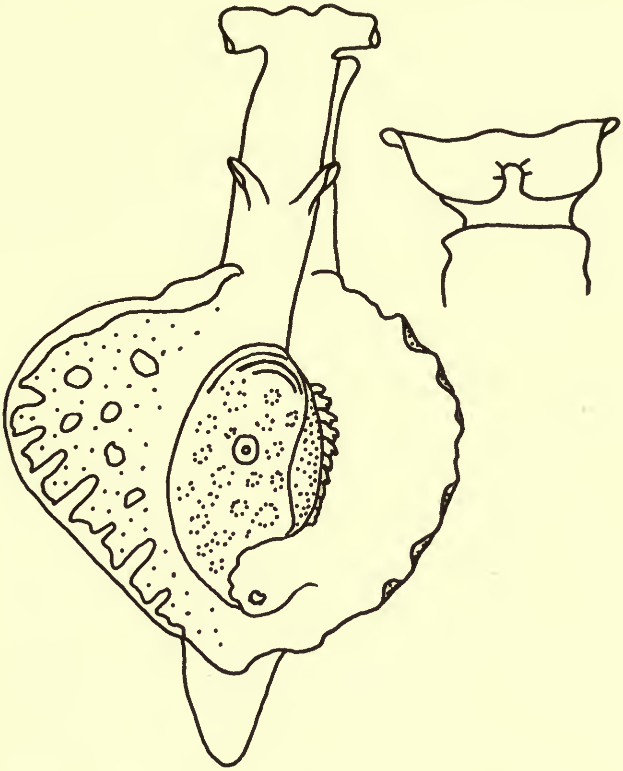

FIG. 22. *Aplysia extraordinaria.* Dorsal view of the type specimen. The sinuous edge of the parapodium is shown on the right, the pattern of the inner side on the left, with its light rim. The right mantle edge has been reflected to show the ctenidium and the purple gland. The small papilla on the mantle is ringed, and the mantle is blotched with brown and white, but is lined near the edge. × $\frac{2}{3}$. An enlarged view of the mouth region is alongside.

Shell (Text-fig. 23*b*) removed from the type. Said by Allan to be 75 × 56 mm. In another specimen it measured 45 × 36 mm., and is therefore broadly ovate, with strong concentric lines, without spire, anal sinus shallow. Deep yellow in colour.

The jaws are curved plates, composed of closely packed rods, rather short, truncate at the apex.

Radula (Text-fig. 23*d*) with about 70 rows and a formula 32.1.32. Rhachidian tooth pale, weak and sunken, with a short and not broad basal plate, almost straight posteriorly and with a short cusp with fine denticulations. The first lateral has a narrow basal plate enlarging to a swollen head, short cusp and numerous denticles on both sides, the lateral basal denticle larger than the others and its edge cut into denticles ; this feature is repeated throughout, the denticulations becoming highly elaborate and irregular, though the cusps remain of moderate length. The three outermost teeth are vestigial.

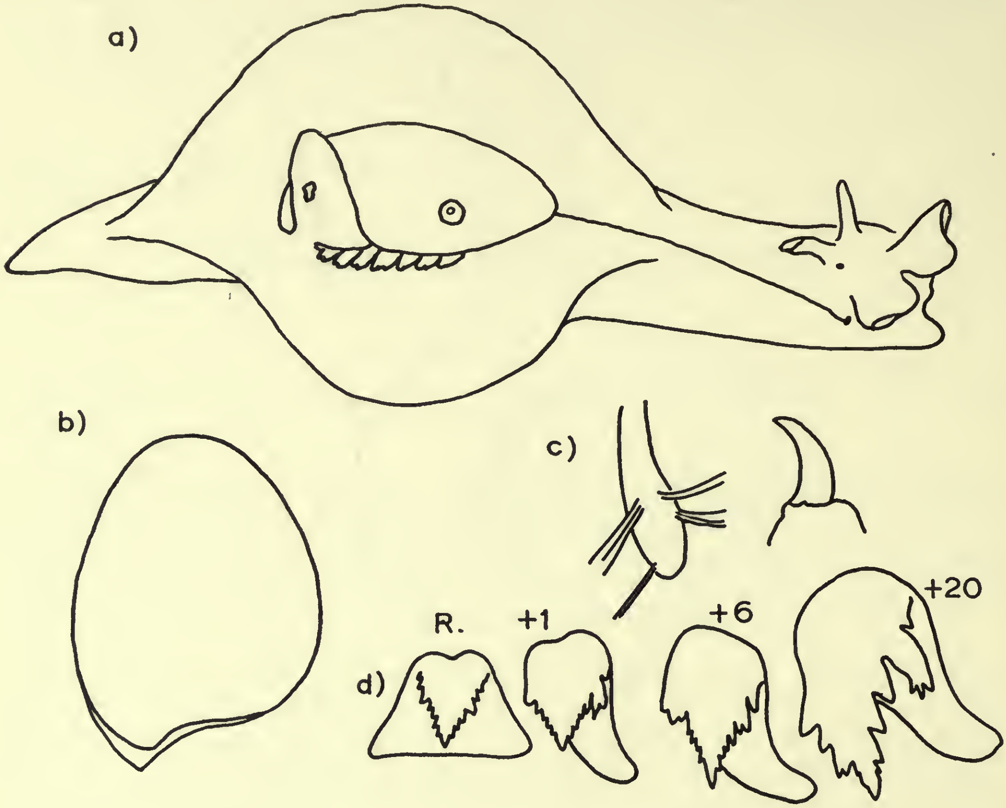

FIG. 23. *Aplysia extraordinaria.*

(*a*) Half lateral view of a specimen in the B.M. (N.H.) collection to show the elongation of the neck region, the large parapodia and the tall, leaf-like anal siphon. The head is somewhat contracted. × $\frac{2}{3}$.

(*b*) Shell in dorsal view. × $\frac{2}{3}$.

(*c*) Penis sheath with its retractor muscles, and the extruded penis. × $1\frac{1}{2}$.

(*d*) Radular teeth. Rhachidian, first, sixth and 20th lateral teeth × 80, the last enlarged. × 140.

Caecum small, lying flat on the surface of the digestive gland. In the type specimen it is corrugated and its tip is recurved, but in another specimen it remains straight.

Cerebral ganglia fused, visceral joined and spread along the visceral cords.

SPECIFIC CHARACTERS

Large Aplysias, not bulky but slender and active. Deep brown with black reticulations and scattered spots and blotches. Skin smooth, soft and flabby. Head small with slender neck. Rhinophores slender, close together. Foot long and narrow, tail long. Parapodia large, rounded, natatory, meeting low down posteriorly. Mantle small, with contractile foramen and tall anal siphon. Purple secretion probable. Opaline gland simple, small, multiporous. Shell broadly ovate. Radula with elaborate primary and secondary denticulations.

South Pacific area.

Aplysia (Varria) fasciata Poiret, 1789 : 2

Text-fig. 24

SYNONYMY : *alba* Cuvier, 1803 : 295 ; Rang, 1828 : 60, pl. 15.
cameliformis Locard, 1886 : 66.
camelus Cuvier, 1803 : 295 ; Rang, 1828 : 60, pl. 15.
depilans ; de Blainville, 1823 : 286.
leporina Rang, 1828 : 54, pls. 6 and 7.
lepus Philippi, 1844 : 99.
limacina de Blainville, 1823*b* : 287 ; *a* : 328 ; Blochmann, 1884 : 29
marmorata de Blainville, 1823*b* : 286 ; *a* : 326.
neapolitana and *napolitana* delle Chiaje, 1823 : 31, 39, 70.
radiata Crouch, 1826 : 44.
sicula? Swainson 1840 : 247, fig. 45.
vulgaris de Blainville, 1823 : 285.
Dolabella lepus Risso, 1826 : 44.
Lepus marinus Rondelet, 1554 : 520.
Lernaea Bohadsch, 1761 : 49. Not binominal, but two kinds are recognized, one of which is *fasciata* (see p. 357).
Siphonota lobiancoi Mazzarelli, 1890 : 42 (probably a hybrid).

DISTRIBUTION. Red Sea, Mediterranean, Atlantic coasts from France to Angola (Portuguese West Africa), taken in Morocco, Senegal, Ghana and the Canary Islands. Rarely occurs on the southern coasts of Britain.

MATERIAL EXAMINED. Specimens from the above areas.

This handsome species was described by Poiret from the coast of Barbary in its black, scarlet-bordered form. Rang (1828, pls. 6 and 7) gave good coloured figures of it, and on pl. 15 and 15 bis. as *camelus*, *alba* and *napolitana*. Several authors confused it with *depilans*. Pilsbry reverted to Linnaeus's name *leporina*, because, he says, " Rondelet's figure and description of the coloration agree well with this species and not with any other European Sea Hare ". The International Commission on Zoological Nomenclature, however, (Opinion 200, 1954 and Opinion 354, 1955) validated the name *fasciata* Poiret, 1789, owing to confusion between *leporina*, *depilans* and the nudibranch *Tethys leporina* (now *fimbria*).

Large Aplysias, reaching nearly 400 mm. when alive. High and narrow, a preserved specimen measuring 138 mm. long, 60 mm. wide and 90 mm. high. Skin soft and firm. Colour velvety black all over, or spotted with clusters of white and grey flecks and with a red border to the parapodia, cephalic tentacles and rhinophores, fading to a light rim with preservation. The black colour is marked on the mantle, ctenidium and anal siphon, but the mantle cavity floor and foot are usually less heavily pigmented. Paler specimens may be yellow, with round brown or black spots, and occasionally white individuals occur. All colour may disappear with long preservation.

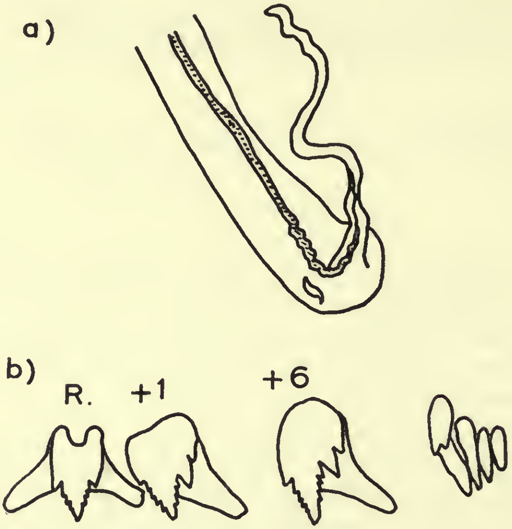

FIG. 24. *Aplysia fasciata.*

(*a*) Penis sheath opened longitudinally to expose the long, filiform penis. The seminal groove is indicated but not continued to the tip of the penis owing to the narrowness of the latter. A small flap lies at its base. × 2.

(*b*) Radular teeth. Rhachidian, first, sixth and outermost lateral teeth. × 80.

Head large, neck short owing to the forward position of the parapodia, but capable of considerable extension. Cephalic tentacles well developed but not long, rolled at the edges, fimbriated on the unusually large rounded extensions to the ventral sides of the mouth slit. Eyes small. Rhinophores slender, small, acutely pointed, slit for only a short distance, the rims of the slit crimson or pale, set close together, only about 9 mm. apart.

Foot narrow, elongated, the lateral edges approximating towards one another as in *punctata*. Front edges rounded, tail short, pointed. Penis (Text-fig. 24*a*) long and slender, filiform, unpigmented. Rang (1828, pl. 7) gave a good figure of it. Distal (bulbous) portion of the sheath small, smooth-lined, with a flap-like ingrowth alongside the sperm groove but not touching it. Parapodia very large, mobile, natatory, arising close together about 20 mm. apart, rounded, tall, with smooth borders, meeting low down on the tail and so narrow here that they are sometimes described as free. The mantle cavity is thus open posteriorly. The parapodia will close completely over the mantle, leaving the anal siphon projecting.

Mantle large, foramen a small flat hole, usually rayed, and tubular if much contracted. Purple secretion exuded. Anal siphon large, broad, tubular.

Mantle cavity widely open. Ctenidium large and thick. Opaline gland compound, compact, with a small round aperture. Genital aperture oblique, fimbriated.

Shell about 70 × 50 mm., broadly ovate, concave, firm, without spire, anal sinus short and not deep.

Jaws rectangular, rods elongate, curved at the tips.

Radula (Text-fig. 24*b*) large, reaching a formula of 80 × 50.1.50. Rhachidian tooth of the same colour as the laterals, not pale or sunken, its basal plate of moderate size, the head tall and narrow, the cusp longer than the plate, rounded, with numerous weak, irregular denticles, the basal ones only slightly larger than the others. First lateral with curved tapering plate, moderately broad head and the usual denticles, a lateral basal one enlarged. Along the row the plates remain tall and narrow, the cusps lengthen but rarely exceed more than half the length of the plate and the denticles become stronger, often with secondary denticulations of the large lateral basal denticles and the addition of others near the head. About four teeth at the end of the row are vestigial.

Caecum tip visible on the surface of the digestive gland.

Cerebral ganglia small, fused.

SPECIFIC CHARACTERS

Large, narrow and high Aplysias, typically black with scarlet rims to the parapodia and tentacles. Head large, with fimbriated cephalic tentacles, narrow foot with pointed tail, penis filiform, white, parapodia large, natatory, meeting low down on the tail, mantle with small flat foramen, purple secretion, compound uniporous opaline gland, shell broadly ovate, radula large, all the teeth denticulate.

East Atlantic, from France to Angola ; Mediterranean and Red Seas.

References (see also synonyms)

Bosc, 1802 : 63, as *Laplisia*.
Cantraine, 1840 : 68.
Carus, 1889 : 196.
Eales, 1957 : 179, as *leporina*.
Engel, 1934 : 85, 88.

Grigg, 1949 : 796, as *limacina.*
Mazzarelli, 1893 : 33, as *Siphonota limacina.*
Odhner, 1932 : 27, as *leporina.*
Pilsbry, 1895 : 72, as *Tethys leporina.*
Rang, 1828 : 54, 60, pl. 15 (as *alba*, *camelus*).
Risbec, 1931 : 68.
Vayssière, 1885 : 54, 60 ; 1935 : No. 20 (not paginated).
Vérany, 1853 : 390.

Aplysia (Varria) gigantea Sowerby, 1869, pl. 1

Text-fig. 25

SYNONYMY : *A. tasmanica* Tenison Woods, 1876 : 156.

DISTRIBUTION. Australian region—West Australia, Abrolhos Islands, New South Wales, Tasmania.

Sowerby named the species from the shell. O'Donoghue (1924) described specimens from near Fremantle, Australia, and these are now in the British Museum (Natural History).

MATERIAL EXAMINED. O'Donoghue's topotypes (B.M. (N.H.)), 1923. 1.26.10–11.

Aplysias of enormous size, reaching 600 mm. in length, but shrinking to much less when preserved. 150 mm. long × 65 mm. wide × 60 mm. high is an average preserved specimen. Body stout and high. Colour and markings variable, background colour dark umber brown to purplish green, with black spots, branched black lines and blotches of light, almost white, areas. The edges of the parapodia may be banded vertically, both inside and out, with alternating bands of white and dark, together with similar blotches of lighter colour, and there is a fine reticulation extending to the edge externally (Text-fig. 25, *b*, *c*). Foot greyish black. Mantle floor and ctenidium usually unpigmented or slightly pigmented. On contracting, the soft fleshy skin assumes a crocodile-skin pattern of flattened areas interrupted by furrows. This is exhibited by small as well as by full grown specimens, and is characteristic though not unique.

Head and neck long. Cephalic tentacles very large, rolled laterally and continued to the sides of the mouth. Rhinophores long and linear, set close together.

Foot broad, especially anteriorly, where it is expanded at the lateral borders and measures 85 mm. wide in a specimen only 150 mm. long (Text-fig. 25*a*). The tail has similar but smaller expansions. Edges of the foot wrinkled, foot sole very muscular, contracting to the crocodile-skin pattern. Penis very broad and stout, short and flat. Parapodia high and well developed, mobile and natatory, rounded in shape, with thin irregular edges. They commence far forward and stand straight up. Posteriorly they are united low down on the foot, forming a spout-like projection of the mantle cavity floor. The dorsal slit is wide open, exposing both mantle and ctenidium.

Mantle large, thin, perforated by a minute foramen on a low papilla, sometimes wrinkled radially. Anal siphon large and broad. Purple glands present.

Mantle cavity widely open, large. Ctenidium very large and protruding. Opaline gland compound with one aperture. Genital aperture smooth or slightly fimbriated.

Shell large. Sowerby figures a dried specimen measuring 96 × 79 mm. It is thin, transparent, pale yellow, concave, the apex a little incurved, the anal sinus long and shallow. Calcareous matter is present during life.

Jaws oblique, composed of slender, curved rods of moderate length.

Radula 15·5 × 14·5 mm., very strong. O'Donoghue (1924) gives 85 rows and formula 59.1.59. Rhachidian with short broad basal plate, very short cusp bearing feeble denticles. First lateral with short plate and cusp, but very wide head, its denticles feeble, but of the usual pattern. Outer laterals may become smooth except for one side denticle on a straight slender cusp. The basal plates of the laterals are squared off and packed in close lines, but the last six or eight teeth are more slender, the outermost three being vestigial.

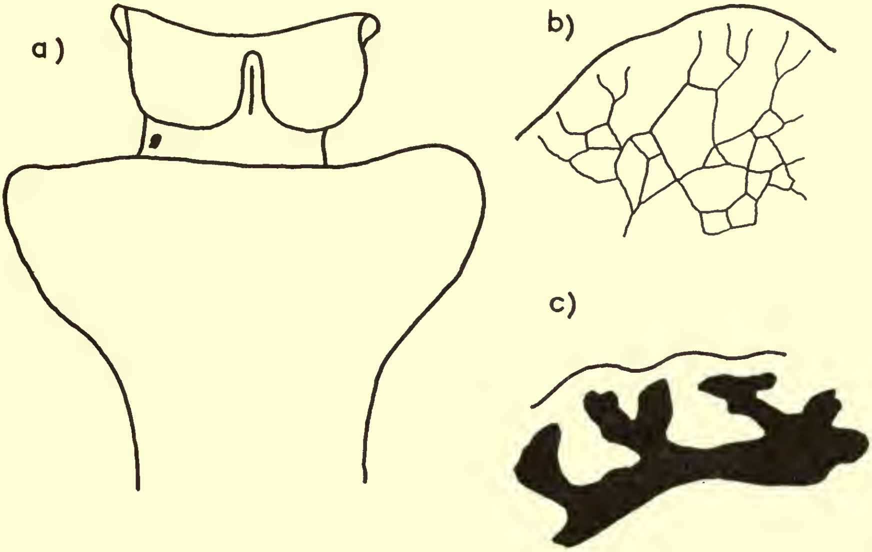

FIG. 25. *Aplysia gigantea.*

(*a*) Head and foot in ventral view to show the large lateral wings on the foot. $\times \frac{2}{3}$.
(*b*) Portion of the outer side of the parapodium to show the fine reticulations.
(*c*) Inner side of the parapodium, with branched bands of black on a light ground.

The inflated tip of the caecum just reaches the surface of the digestive gland.

Cerebral ganglia completely fused, and also the visceral pair.

SPECIFIC CHARACTERS

Large size, smooth skin contracting to a crocodile-skin pattern, large cephalic tentacles, foot expanded laterally anteriorly, high rounded parapodia joined low down on the foot posteriorly, minute mantle aperture and papilla, compound uniporous opaline gland, large rather shapeless shell, numerous closely packed radular teeth with feeble denticulations.

Australia and islands off its coasts.

References (*see also synonym*)

Allan, 1950 : 213.
O'Donoghue, 1924 : 528, as *Tethys.*
Pilsbry, 1895 : 102, as *Tethys.*

Aplysia (Varria) gracilis sp. nov.

Text-fig. 26

DISTRIBUTION. Red Sea.

MATERIAL EXAMINED. A single specimen, the type, B.M. (N.H.), 1907.11.15.29), presented by His Excellency the Minister of Education to the Government of Egypt, and collected near Gemil, Lake Manzaleh in 1907.

A small Aplysia, the preserved specimen measuring 45 mm. long × 25 mm. wide × 21 mm. high, much contracted to the " sitting hare " position. Skin soft, mottled with brownish black and grey on a lighter greenish grey background. There are a few solid spots on the sides. The mantle has blotches of pigment and there are faint markings inside the parapodia, mostly vertical bands of light and dark colour. The tentacles, mantle cavity floor, ctenidium and foot are colourless. The rims of the parapodia and anal siphon are light and devoid of pigment.

Head and neck small. Cephalic tentacles rolled and continued forwards to the lower sides of the mouth. Eyes small but plainly visible. Rhinophores close together and slit almost to their bases, small and conical.

Foot narrow, not tough, 43 mm. long and only 8 mm. wide anteriorly, rounded at the front edges, furrowed longitudinally and prolonged into a short pointed tail. It is sharply marked off from the pigmented side of the body by a small flange. Penis slender and tapering but not very long, the sheath small and smooth-lined distally. Parapodia fairly large and thick but not high, arising far forwards on the neck, sloping backwards, with pale sinuous fimbriated edges, to meet low down on the foot posteriorly, so that the mantle cavity is open and flat.

Mantle small and thin, measuring 20 × 11 mm. There is a small aperture on a papilla. Anal siphon wide and high, directed towards the opening in the parapodia (i.e. backwards) in the specimen. Mantle glands well developed, presumably secreting purple.

Mantle cavity small, ctenidium small and neat. Opaline gland compound, with a single large circular aperture. Genital aperture thin, oblique, pigmented, deeply crescentic. Genital groove shallow and colourless.

Shell small, ovate, delicate, measuring 18 × 14 mm., rather flat. Calcareous lining present. There is hardly any turn over at the apex and the anal sinus is shallow.

Jaws pale and delicate, the rods moderately tall, broadened a little at the tips and slightly curved.

Radula not large, almost square, 4 × 4 mm., with a formula 40 × 21.1.21. It is the most elaborate of all the species of the genus (Text-fig. 26). Rhachidian tooth with a short broad basal plate, slightly incised on its posterior border, but becoming more hollowed out in older teeth. Cusp narrow, at first rounded, then acuminate, longer than the plate, with numerous, short, irregular denticles of which the basal pair are as usual larger than the others. The first lateral has a narrow out-turned plate, large head and more regular denticles, the two outer basal ones being larger than the others and the penultimate one very stout. The cusps increase in length up to about the middle of the row, and their denticles become very large and deeply cut. Mesially there are two small denticles and one larger basal denticle, laterally up to nine denticles, the longest and broadest being the seventh. The last four teeth are degenerate.

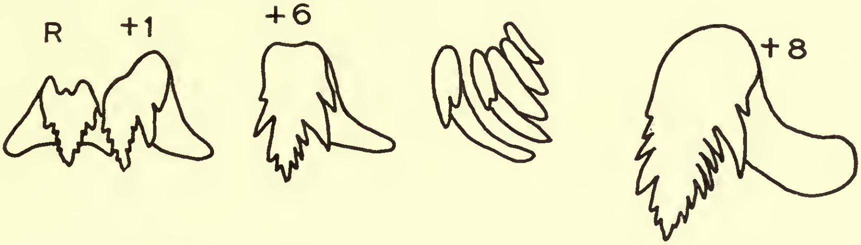

FIG. 26. *Aplysia gracilis*. Radular teeth. Rhachidian, first, sixth and five outermost lateral teeth. × 80. Eighth lateral enlarged. × 132.

Caecum exposed and lying flat on the surface of the digestive gland.

Cerebral ganglia joined, visceral cords short and the ganglia joined but distinct.

SPECIFIC CHARACTERS

Everything about this species is neat and dainty. The specimen is probably not full grown. Small, with mottled and spotted skin, narrow foot, slender pointed penis, fimbriated parapodia joined low down behind, minute papilla on the mantle, compound uniporous opaline gland, delicate oval shell with feeble apex and anal sinus, highly elaborate radula with deeply cut denticulations.

Red Sea.

Aplysia (Varria) inca d'Orbigny, 1837 : 207

DISTRIBUTION. Recorded from Callao Bay, near Lima, Peru.

MATERIAL EXAMINED. The type (1834) and a second specimen collected by Eydoux & Souleyet in 1838, now in the Muséum d'Histoire naturelle, Paris, were examined. Good coloured figures were given by d'Orbigny and reproduced by Pilsbry (1895). Both the specimens in the Paris Museum, however, have lost their colour and are much reduced in size ; neither has a radula, the type has had the shell removed, and the second specimen is without the penis.

The type specimen now measures 60 mm. long, 17 mm. wide and 26 mm. high, the small mantle is 24 × 13 mm., the foot 54 × 13 mm. D'Orbigny described the living animal as large (200 mm.), flabby and swollen. The cephalic tentacles in his figure are very wide and rolled, the rhinophores set well back and close together, conical, slit. Eyes plain. Neck shorter than the distance between the cephalic tentacles and the rhinophores. Foot narrow, with pointed tail. Parapodia large, united posteriorly. Mantle smooth, with a small round aperture and long, wide and thin anal siphon. Animal violet, with round white spots on the sides and in a row on each side of the head. Inner sides of the parapodia with a narrow border of clear rose violet and large rounded and angular white blotches on a purple brown ground. Mantle violet.

To this may be added : Penis short, broad, tapering and flat at the tip. Penis sheath smooth-lined distally. Parapodia smooth edged, joined to form a low wall about 10 mm. high around the mantle cavity posteriorly.

Opaline gland small, partly compound, but with a group of apertures arranged in a circle.

Shell broadly ovate with distinct anal sinus.

Caecum small, just breaking surface on the digestive gland.

Cerebral ganglia joined, visceral ganglia distinct.

SPECIFIC CHARACTERS

Large size, purple coloration with white spots, soft flabby skin, capable of great contraction, wide cephalic tentacles, short broad tapering penis, narrow foot and pointed tail, large parapodia united to form a low wall posteriorly, small mantle aperture, partly compound opaline gland with a group of apertures. Radula unknown.

Eastern South Pacific.

Reference

Pilsbry, 1895 : 87, as *Tethys*.

Aplysia (Varria) keraudreni Rang, 1828 : 59, pl. 13

Text-fig. 27

SYNONYMY : *lessoni*? Rang, 1828 : 60, pl. 14. See below.

DISTRIBUTION. The species has been recorded from the South Pacific only. Rang's single specimen came from the Society Islands.

MATERIAL EXAMINED. Five specimens from the Portobello Marine Biological Station, Otago, New Zealand, and one from Wellington Harbour ; another, juvenile, from the Kermadec Islands. A small specimen, much contracted, but probably belonging to this species, came from Sydney, Australia.

Rang gave a good figure of this large and handsome species, copied by Pilsbry (1895 : pl. 39).

Mature specimens attain 250 mm. or more in length, preserved about 188 mm. long, 75 mm. wide and 80 mm. high. Thick and fleshy, with rather small head, but very large mantle region and visceral hump. Olive green to dark brownish black, with scattered brown spots or blotches and reticulate black lines all over. There may also be white areas. Cephalic tentacles, rhinophores and edges of the parapodia with light brown or white margins. Mantle dappled light and dark. Inner sides of the parapodia with irregular light flecks on a dark ground. Skin soft, but when contracted may form crocodile-skin patterns or become firm and tough. All colour may disappear with preservation.

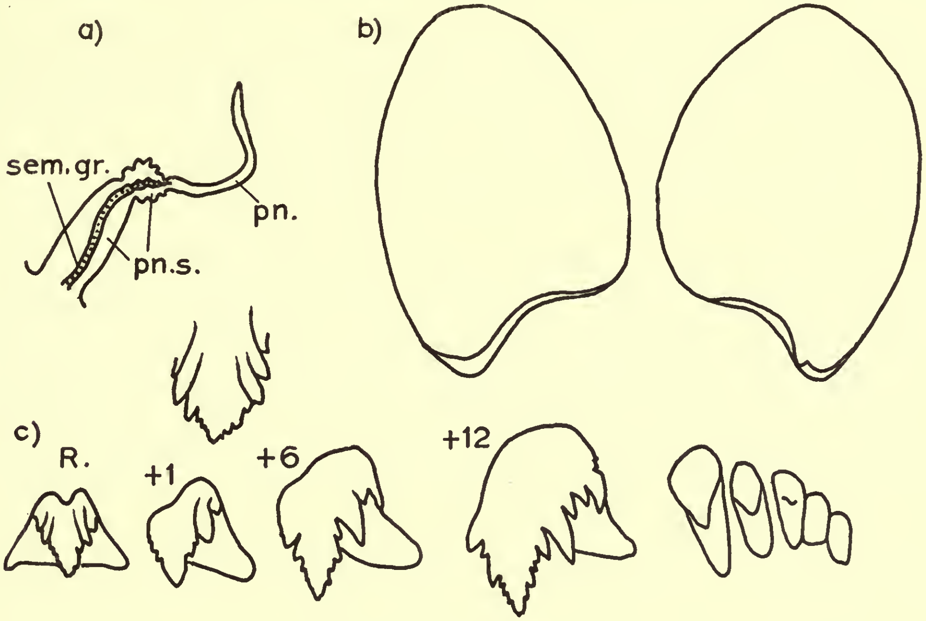

FIG. 27. *Aplysia keraudreni.*

(*a*) The extruded penis, showing its filiform shape and the two portions of the sheath, the distal part of which is white and fibrous, the proximal part thick, dark and muscular. The seminal groove has been sketched as far as the penis base only. × 2.
(*b*) Shell in dorsal and ventral views. × $\frac{2}{3}$.
(*c*) Radular teeth. Rhachidian, first, sixth, 12th and outermost lateral teeth. × 80.

Head rather small but broad, neck short, thick. Cephalic tentacles large, rolled on the edges, rounded in front, joined to the sides of the mouth slit, fimbriated. Eyes small. Rhinophores slender, pointed, close together, slit half-way and dark within the slit.

Foot broad, 50 mm. wide in the 188 mm. specimen, thick, spongy, prolonged into a bluntly pointed tail about 28 mm. long. Penis and its sheath characteristic and easily eversible. Penis (Text-fig. 27*a*) white, filiform, the distal bulbous portion of the sheath also white, thin-walled, the proximal muscular portion dark, rugose. Parapodia large, rounded, frilled on the edges or smooth according to the degree of contraction. Only 23 mm. apart in front, rather thick, freely mobile, natatory, meeting low down and hardly joining on the root of the tail, forming a flat platform, or a low wall about 10 mm. high around the mantle cavity.

Mantle very large, 70 × 52 mm., thick, with small, round, finely rayed aperture. Anal siphon broad, frilled but not tall, tubular. Mantle glands well developed, exuding purple. Mantle border wide, overlapping the ctenidium.

Mantle cavity large, ctenidium also large, with some pigment. Opaline gland simple, with large vesicles and numerous apertures, the gland cells tending to join anteriorly by fusion of their ducts and forming an anterior aperture larger than the others. Genital aperture small, smooth, not covered by the mantle or pigmented.

Shell (Text-fig. 27*b*), large, 70 × 50 mm., broadly oval, shallow, with weak apex just recurved and dorsal border bent over. Anal sinus short, thick walled, shallow, with rounded outer angle. Lines of growth well marked.

Jaws long and rectangular, 10 × 2·5 mm., rods slender, curved or straight, of moderate length.

Radula 13 × 10 mm., with a formula 55 × 35.1.35 (Text-fig. 27*c*). Rhachidian tooth pale, sunken, with small and rather narrow basal plate, excavated in front, straight behind. The cusp is equal to or a little longer than the plate, rounded, with irregular denticles, fluted, the basal denticles larger than the others. First lateral with broad, elevated head, similar denticles laterally and short rounded cusp, also fluted. The remaining teeth with broad low heads, lengthening and narrowing cusps and great exaggeration of the lateral denticles in number, size and irregularity. Secondary denticulations occur in some. The outermost three to four teeth rectangular and vestigial. A very elaborate radula.

Caecum just appearing on the surface, slightly bent at the tip.

Cerebral ganglia completely fused, visceral with large nerve cells making them appear knobbly.

Specific Characters

Large handsome Aplysias, with fimbriated cephalic tentacles and parapodia. Colour dark, with spots and blotches of a darker colour, but with light edges to the tentacles and parapodia. Head rather small, visceral region exceptionally large, with wide overhang to the mantle, where the purple glands lie. Foot broad, with blunt tail. Penis white, filiform, penis sheath partly white thin, partly dark muscular. Parapodia large, natatory, meeting low on the tail. Mantle aperture small, rayed. Opaline gland simple, multiporous. Shell large, broadly ovate, shallow, apex narrowed. Radula elaborately denticulate.

South Pacific.

References (*see also synonym*)

Lesson, 1830 : 294.
Mazzarelli & Zuccardi, 1892 : 11.
Pilsbry, 1895 : 95, as *Tethys*.

Note. Angas's *Syphonota keraudreni*, 1867 and Sowerby's *A. keraudreni* from Australia are probably *A. dactylomela*.

I have not seen *A. lessoni* Rang, 1828 : 60, recorded from Peru, and by Mazzarelli & Zuccardi (1892 : 11) from Honolulu. From the little that is known of it, I suspect that it is *keraudreni*, with which it agrees in size, shape, large, rounded cephalic tentacles, broad foot, large parapodia united low behind, large mantle with tubular aperture and shape of the shell. Mazzarelli & Zuccardi added the information that the opaline gland is simple, multiporous, the radula with 30 rows and formula 45.1.45. Their figure of the radula is similar to that found in *keraudreni*.

Aplysia (Varria) kurodai Baba, 1937 : 213

SYNONYMY : Takahashi's *Tethys punctata* Cuvier, from Formosa (1934 : 357) is probably this species.

DISTRIBUTION. Japan, Formosa, Asiatic Mainland. Baba states that it is a common species in Japan and Formosa.

MATERIAL EXAMINED. Seven good specimens, hitherto unnamed, have been in the British Museum (Nat. Hist.) collections since 1921 and were collected by A. V. Insole at Misaki, Japan. The Paris National Museum has 18 specimens from Japan, collected in 1903, and two from the mainland of Manchukuo, dated 1844.

Baba (1949 : pl. 14) gave coloured figures of the species, and a sketch of the radula (p. 25). In 1956 he described the egg strings as pink or yellow, with 15–30 eggs in each capsule.

Large Aplysias, attaining 400 mm. in length. Colour variable, but typically dark, brown or purplish black, with small irregular greyish mottling on the sides and mantle, clear blotches on the inner sides of the parapodia and sometimes black edges. Foot dark, mantle cavity floor and ctenidium not pigmented. The general appearance is that of a very heavily pigmented animal. Skin soft, but not flabby. On contracting the species assumes the sitting hare position. Baba's figure shows it to be a mobile species.

Head and neck long but not large. Cephalic tentacles more than double the length of the rhinophores, sinuous on the edges, folded. Rhinophores narrow, pointed, but stout when contracted.

Foot large, broad, 22 mm. wide in a 62 mm. specimen, tough, truncate anteriorly, much wrinkled in contraction, tail short, obtuse. Penis and sheath small, penis filiform. Genital groove delicate. Parapodia rounded, thin, flexible, black and irregular on the edges, joined low down on the tail, often appearing to be quite free. They hardly cover the mantle.

Mantle oval, rather small ; a small foramen opens on a papilla, but is not easily seen owing to the heavy pigmentation and mottled pattern of this area. Anal siphon short, broad, tubular ; anus with lobed aperture. Purple glands present.

Mantle cavity open. Ctenidium small, opaline gland kidney shaped, simple, multiporous. Genital aperture small, crescentic, smooth.

Shell oval, narrow (30 × 19 mm. in a 62 mm. specimen), rather flat, thin ; apical region weak, but the edge recurved and thickened dorsally ; anal sinus shallow, calcareous matter present.

Jaws dark brown, rods long and curved.

Radula 50 rows, 34.1.34, but Baba gave 70 × 43.1.43. Teeth closely packed. Rhachidian tooth with moderately broad basal plate, incised anteriorly but almost straight posteriorly, with rounded edges. Cusp hardly longer than the plate, but becoming shorter with wear. Denticles irregular. First lateral with broad curved out-turned basal plate, large head and irregular denticles on the cusp, with two larger basal denticles laterally. Sixth lateral with broad rounded basal plate, a longer and sharper cusp, but with similar irregularities in the denticulation. Last three teeth vestigial.

Caecum very large, curved, swollen at the tip.

Cerebral ganglia fused, visceral fused.

SPECIFIC CHARACTERS

Large Aplysias, with heavy pigmentation, mobile. Penis filiform ; foot broad ; mantle papilla small ; mantle glands secreting purple ; opaline gland simple multiporous ; shell flat, thin, radula large with numerous teeth, irregular denticles ; chief ganglia fused.

North-west Pacific.

Reference

Baba, Hamatani & Hisai, 1956 : 216 (breeding habits).

Aplysia (Varria) maculata Rang, 1828 : 58, pl. 12

SYNONYMY : *eusiphonata* Bergh, 1908 : 9.
gargantua Bergh, 1908 : 5.
gilchristi Bergh, 1908 : 2.
poikilia Bergh, 1908 : 10.
Tethys poikilia O'Donoghue, 1929 : 21.
tigrina ; Quoy & Gaimard, 1832 : 308 (*non* Rang, 1828).
tigrinella Gray, M.E., 1850 : 97, new name for *A. tigrina* Q. & G.

DISTRIBUTION. Confined to the western part of the Indian Ocean : Mauritius, Réunion, Lourenço Marques, South Africa.

SPECIMENS EXAMINED. Several from South Africa, sent by Dr. Macnae.

Rang gave good figures of this species, copied by Pilsbry (1895 : pl. 17). In 1955 Macnae published a detailed account of its structure and a useful compilation of the synonyms. He decided that Quoy & Gaimard's *tigrina*, renamed *tigrinella* by Mrs. Gray, and re-examined by Mme. Pruvot-Fol (1934 : 39), is a synonym of *maculata*, thus clearing up the confusion arising from Quoy & Gaimard's misuse of Rang's name. The papillae shown in their figure (see Pilsbry, 1895 : pl. 16) were not mentioned in the description and may have been added mistakenly by the engraver. Papillae, however, do occasionally occur in preserved specimens of other species, cf. *A. parvula* above (p. 288).

Rather large Aplysias, with long neck and ovate posterior region, ending in a narrow pointed tail. May attain 300 mm. in length, but a preserved specimen shrinks to about 170 mm. long, 34 mm. wide and 77 mm. high. The skin is soft and flabby. Colour very variable, usually brownish olive, with irregular black and light spots, often confluent in patches on the head, sides of the body and inner sides of the parapodia. A few spots on the foot and mantle, the latter sometimes with irregular radiating lines of black. Some specimens are grey all over, without black pigment, or some of the spots may have clear centres and become rings, but this is not common. The parapodial rims are unpigmented or white.

Head and neck narrow and long, usually narrowed behind the head. Cephalic tentacles well developed, capable of considerable expansion, not fimbriated, rolled on the edges and continued to the borders of the mouth. Eyes small. Rhinophores slender, tapering, close together and well back.

Foot narrow (only 20 mm. broad in a specimen 85 mm. long). Rounded anteriorly, prolonged posteriorly into a pointed tail. Lateral edges well defined and usually projecting as a flange all round. Penis short, broad at the base, but tapering to a slender point, the sperm groove running straight to its apex. Parapodia large, extending from close behind the rhinophores to the root of the tail, thin, tall and wing-like, flexible but not fimbriated. Macnae states that the young animal can swim. Anteriorly the parapodia slope backwards, as Rang's figure showed ; posteriorly they join low down, or may appear free. The mantle cavity is thus open at both ends, the dorsal slit is wide open, but may be closed by folding over of the parapodia.

Mantle large and thin. Mantle foramen small, usually flat, with radiating black lines around it. Anal siphon large, tubular, leaf-like, with a sinuous edge ; it has a tendency to slope backwards, as in many species in which the parapodia meet low down on the foot. Purple glands are present.

Mantle cavity large and flat, the ctenidium large and unpigmented. Opaline gland simple and pear-shaped, multiporous. Genital aperture anterior to the mantle, plain and crescentic.

Shell elongated (measuring 34 mm. × 22 mm. × 4 mm. in a 67 mm. specimen), thin and shallow, without a spire, the apex being only slightly recurved. Calcareous matter is present in the fresh condition. The anal sinus is short and shallow.

Jaw plates well developed, dark brown in colour. The rods long and curved, with pointed or truncated tips.

Buccal mass relatively large. Radula with about 65 rows and a formula up to 38.1.38. The rhachidian tooth is of moderate height and breadth, its basal plate excavated in front and almost straight behind, the cusp about as long as the plate, with deeply cut denticles, the basal pair of which are larger than the others. Older teeth may become fluted and lose their denticles. The first lateral has a short cusp and the usual denticles. Both the main cusp and the basal denticle become accentuated as the distance from the centre of the row increases, a strong denticle is added mesially and one or more laterally. As the cusp narrows it becomes curved lateralwards, but retains its deeply cut denticles. After about the 24th tooth the cusp shortens, and the outermost six teeth are degenerate, a rather large number for an Aplysia.

Caecum large and inflated at the tip, its blind end exposed on the surface for some distance.

Cerebral ganglia completely fused, forming a flat band. Visceral ganglia joined but distinguishable.

Specific Characters

Small head, long neck, ovate visceral region, widely open dorsal slit, spotted skin, narrow foot with lateral flange and pointed tail, short acuminate penis, mobile parapodia joined or free low down posteriorly, large mantle with small rayed aperture, simple opaline gland with many apertures, delicate narrow shell and radula with deeply cut denticulations.

Western Indian Ocean, from Mauritius to the Cape.

References (see also synonyms)

Deshayes, 1863 : 54.
Krauss, 1848 : 71.
Lamarck, 1836 : 691.
Macnae, 1955 : 231.
Martens, 1880 : 307.
Pilsbry, 1895 : 107, as *Tethys*.
Pruvot-Fol, 1934 : 39, as *tigrinella* Gray, 1850.
Sowerby, 1869 : pl. 6.

Aplysia (Varria) morio Verrill, 1901 : 25

Text-figs. 28 and 29

Synonym : *modesta* Thiele, 1910 : 124, probably a juvenile.

Distribution. First recorded from Bermuda, but occurs from Rhode Island to Florida and Texas on the mainland.

Material examined. Numerous specimens from Bermuda and the eastern seaboard of the United States.

This is a very large but not bulky species. Verrill records a living specimen 400 mm. long and 145 mm. high. A specimen in the Naturhistoriska Riksmuseum, Stockholm (Text-fig. 28) measured 250 mm. long, 65 mm. wide and 110 mm. high, the great height being due to the upward extent of the enormous parapodia, and not to bodily size. These parapodia can be spread widely also, giving a breadth in the

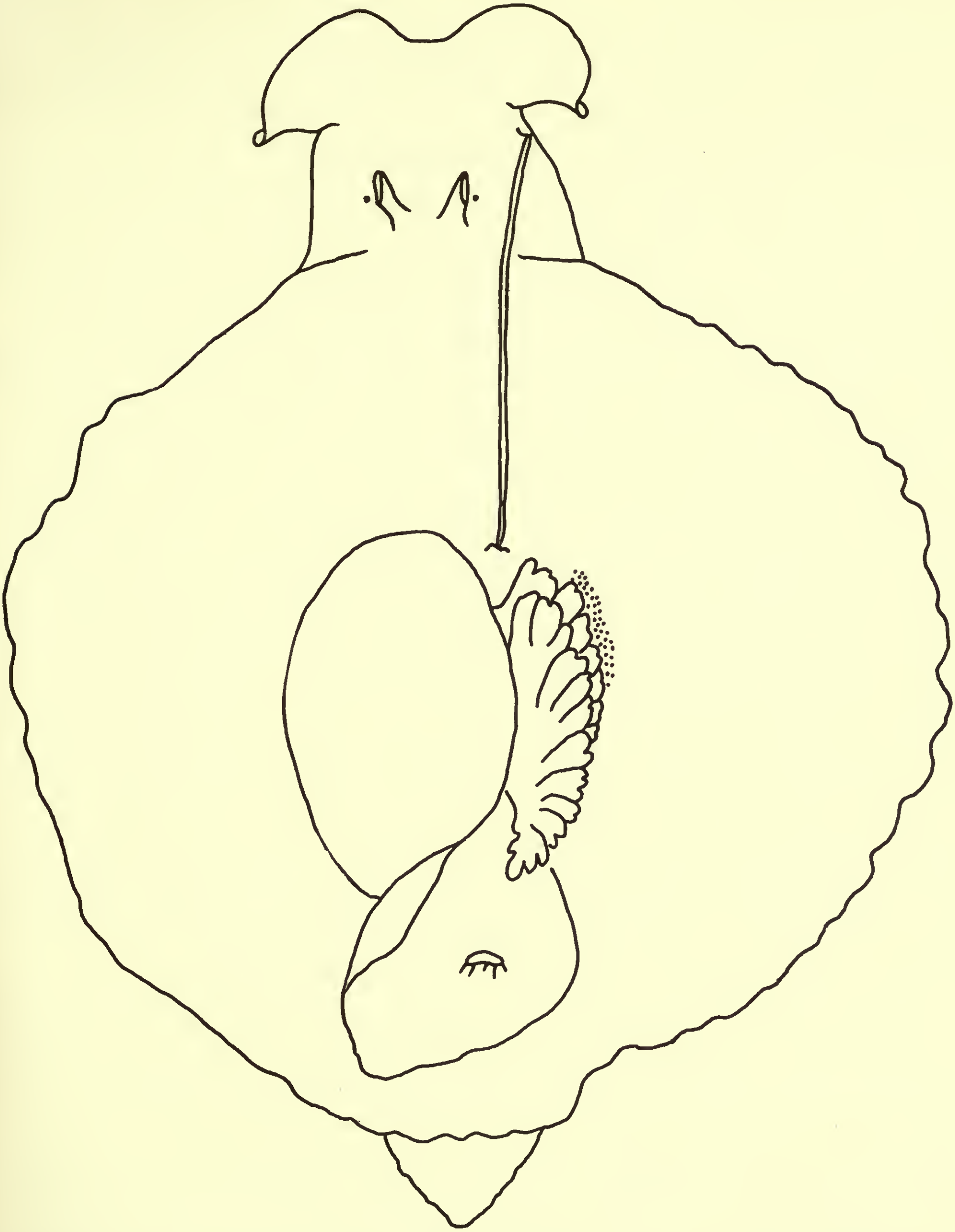

FIG. 28. *Aplysia morio*. Dorsal view to show the wide cephalic tentacles, short neck, enormous parapodia, small closed mantle, large, leaf-like anal siphon, ctenidium and apertures of the opaline gland. From a specimen in the Swedish National Museum, Stockholm, from Bermuda. × $\frac{2}{3}$.

second specimen of 186 mm. The animal is a good swimmer. Dr. R. B. Hill of Bermuda Biological Station writes that he saw it swimming on the surface of the sea. Colour deep umber brown or nearly black, without spots, but with some dark lines or stripes on the head and sides. The foot is dark, the mantle and inner surface of the parapodia very dark, the ctenidium sometimes striped dark brown and light alternately. All parts of the body, including the foot, are soft.

Head and neck relatively short, especially the latter, but they appear wide owing to the lateral extension of the hemispherical cephalic tentacles, which are rolled on their edges and are continued to the sides of the mouth slit. The eyes are small, on light areas of skin, just antero-lateral to the bases of the rhinophores, which are short, rather stout, slit deeply, pointed at the apex and set very close together.

Foot elongated and very narrow, rounded in front, prolonged posteriorly as a short elliptical tail. It is wrinkled and soft, not tough, the edges wavy and well defined. The penis sheath (Text-fig. 29*c*) is anchored by numerous strands of muscle laterally ; its bulbous distal portion is not greatly enlarged, and is dark brown, with a smooth lining. The penis (Text-fig. 29*d*) is short, thick, tapering, curled round at the apex, unpigmented. The enormous parapodia are high and rounded. They commence close behind the rhinophores in the 250 mm. specimen, only 13 mm. behind them and 20 mm. apart, 52 mm. in front of the mantle. The flaps are thin, wide and deep brown inside, without markings, fluted on the edges and joined posteriorly low on the foot where they are tied to the tail by a little keel. They are thus free, flexible and obviously natatory. They expose the whole of the dorsal area, but Verrill remarks that they can overlap in repose.

Mantle relatively small, less than a third the total length of the animal. In young specimens there is a small mantle foramen, but this closes later and in the adult there is no sign of the closure. The anal siphon is large, thin, tubular and leaf-like. Specimens from Florida exhibited a purple colour in the mantle glands, so that purple is secreted by them.

Mantle cavity widely open, ctenidium large and exposed. Opaline gland large, simple, multiporous. Genital aperture hardly covered by the mantle, pigmented, with a frilled edge. The genital groove has a dark overhanging lip, but is itself light.

The shell cavity, as above mentioned, is closed. The shell (Text-fig. 29, *a*, *b*) is long and narrow, without a spire, with a shallow anal sinus, the anterior border not narrowed. The dorsal edge of the apex and sinus are recurved, and one specimen has a hooked apex. The surface in older specimens is ridged concentrically.

Jaws light brown in colour, rounded at the ends and composed of tall curved rods.

Radula (Text-fig. 29, *e*, *f*) large and also light brown. There are about 86 rows, with a formula 56.1.56. Rhachidian tooth short and broad, the head narrow and excavated, the sides of the plate shouldered, the posterior border slightly concave. The cusp is equal to or longer than the plate, finely denticulate, with somewhat larger basal denticles. The first lateral has the usual broad head and an almost triangular plate. The denticulations are numerous and fine, the basal denticles larger laterally and secondarily denticulate in some. Along the row the cusp lengthens

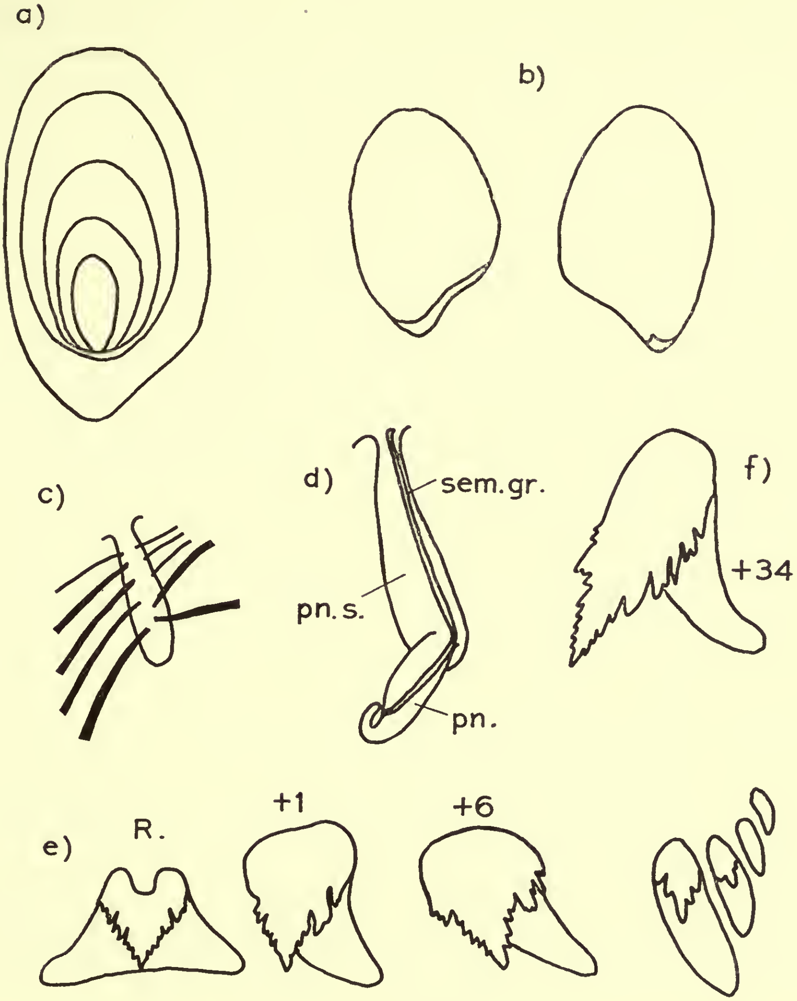

FIG. 29. *Aplysia morio.*

(*a*) Shell in dorsal view. The calcareous matter had been dissolved out in the specimen, leaving only a gelatinous mass under the horny portion. There are strongly marked ridges. $\times \frac{2}{3}$.

(*b*) Dorsal and ventral views of the shell of a younger specimen from Florida, now in the American National Museum, Washington, U.S.A. The concentric ridges are not figured. $\times \frac{2}{3}$.

(*c*) Penis sheath with its numerous anchoring muscles. $\times \frac{2}{3}$.

(*d*) Penis sheath opened to expose the penis and sperm groove. × 1.

(*e*) Radular teeth. Rhachidian, first, sixth and outermost lateral teeth. × 80.

(*f*) Thirty-fourth lateral tooth. × 132.

and narrows, the denticulations increase and involve the large lateral denticles, more being added on their sides. The three outermost teeth are vestigial. The feature of this radula is the extreme denticulation, both primary and secondary.

Caecum large and corrugated, appearing on the surface for 30 mm., lying flat, but inflated at the end. Digestive gland relatively small.

Cerebral ganglia fused to form a band. Visceral ganglia joined.

SPECIFIC CHARACTERS

Large size, deep brown colour, soft skin, wide hemispherical tentacles, narrow foot with short tail, very large, free, thin, natatory parapodia, arising close behind the rhinophores, then becoming wide, rounded and fluted on the edges, to unite low down on the tail. Mantle and visceral regions small. No shell foramen in the adult. Large leaf-like anal siphon, large ctenidium, simple multiporous opaline gland. Shell long and narrow, without spire, strongly ridged, with hardly any anal sinus. Radula with numerous rows and more than 50 teeth on each side in a full row. All the teeth, except the few outermost vestigial ones, with elaborate denticulation. Penis sheath anchored by numerous muscle strands, plain internally; penis short, stout, unpigmented.

Western North Atlantic.

Aplysia (Varria) oculifera Adams & Reeve, 1850 : 64

Text-fig. 30

SYNONYMY : *dactylomela* (pars) ; Macnae, 1955 : 226.
lineolata Adams & Reeve, 1850 : 64.
nodifera Adams & Reeve, 1850 : 64.
Tethys allochroa ; O'Donoghue, 1929 : 19 (*non* Bergh, 1905).
Tethys hirasei Baba, 1936 : 10.

DISTRIBUTION. Red Sea, Seychelles, Persian Gulf, Pakistan, Ceylon, Mauritius, South Africa, East Indies, Formosa, Riu Kiu Islands, Japan, Western Australia, therefore widespread in the Indian and North Pacific Oceans.

MATERIAL EXAMINED. Specimens from the Red Sea, Persian Gulf, Pakistan, East Indies and Western Australia.

Baba (1949 : pl. 4) gave a coloured figure of a Japanese specimen as *hirasei*. In 1956 (p. 216) he described the egg strings as yellowish green, with two to three eggs in each capsule.

Aplysias of medium size, but rather coarse and bulky. Baba (1936) records a specimen 130 mm. long when alive ; preserved, a full grown specimen is about 90 mm. long, 27 mm. wide and 42 mm. high. Slender when young, with a long pointed tail, but the mature specimens are never as large as specimens of *A. dactylomela* with which the species has been confused. Colour pale olive green, dull green, yellowish brown or rich chocolate brown, without radiating lines, but covered all over, except on the mantle and foot, with small black or brown rings, subequal in size and averaging 1 mm. in diameter. The outlines of the rings are neat, occasionally star-like, but not merging into the background as in *A. dactylomela*, nor are they linked by anastomoses. There are numerous rings on the head and even on the tentacles, but no large ring in front of the rhinophores. The centre of a ring may be buff, greenish white or white, and chalk granules may occur in groups between the rings. There may also be dark mottled blotches between the rings. The mantle is speckled or sooty but not rayed. The inner sides of the parapodia are paler, with vertical bars of brownish green alternating with clear areas. The foot is pale. The skin is soft, but firm, and tends to be rough on the mantle.

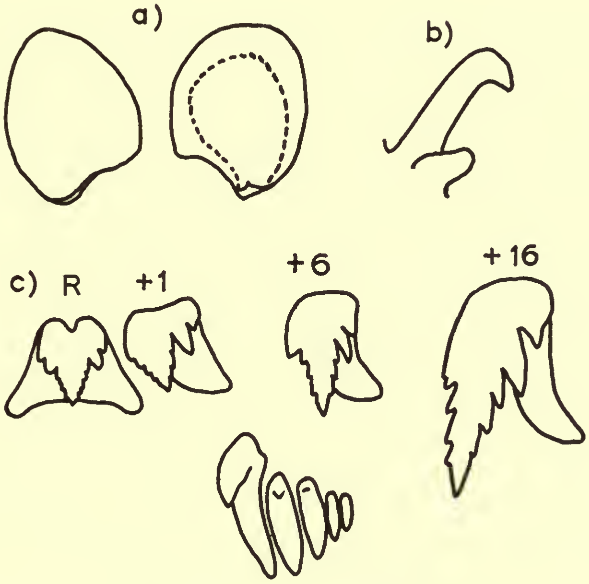

Fig. 30. *Aplysia oculifera.*

(*a*) Shell in dorsal and ventral views. The calcareous layer has been indicated by a dotted line. × $\frac{2}{3}$.

(*b*) Penis extruded, with the flap at its base. × 2.

(*c*) Radular teeth. Rhachidian, first, sixth and outermost lateral teeth. × 80. The 16th lateral enlarged. × 132.

Head and neck elongated, but strongly retractile. Cephalic tentacles large, broad and mobile, short and rolled when contracted. Rhinophores acutely pointed, slender, slit half-way down, strongly contractile and sometimes branched.

Foot moderately broad, rounded anteriorly, rather tough and wrinkled, unpigmented, sharply marked off from the sides of the body, with a pointed tail. Penis (Text-fig. 30*b*) short and broad, but can elongate ; spatulate to pointed at the tip, not spirally twisted, with a flap at the base which is characteristic of the species. Parapodia long, not very high, widely spaced anteriorly, thick, frilled on the edges, coming close together low down on the foot posteriorly, and either free or joined low down, forming a shallow platform. Dorsal slit wide open.

Mantle rather large and tough. Occasionally a papilla is present, or a very small, nearly closed aperture (Baba, 1936). Anal siphon short, broad, tubular, frilled. Purple glands well developed.

Mantle cavity of moderate size. Ctenidium large, without pigment. Opaline gland simple, large, with numerous apertures, but as in other species a group of cells may unite anteriorly to secrete by a common aperture larger than the others. Internally, fibrous bands bind down the gland cells and these have to be dissected off to expose the gland fully. Genital aperture large, with smooth border in the young, but thickened and corrugated in the adult. Genital groove deep.

Shell (Text-fig. 30*a*) varying from narrow to broad, neat, ovate, deeply concave. A firm calcareous lining does not quite reach to the edge of the horny portion. Dorsal edge recurved. Apex small and pointed, but strongly calcified. Anal sinus shallow.

Jaws rectangular, short and wide. Rods of moderate length, loosely packed, tips square or oblique, but not broadened.

Buccal mass rather small for the size of the animal. Radula with about 60 rows, 38.1.38 (Text-fig. 30*c*). Rhachidian tooth with wide basal plate, which in young specimens is deeply excavated posteriorly so that it appears to be resting on two diverging legs, but in mature animals it becomes straight. Head narrow, cusp longer than the base but narrow, with a few fine denticles and two pairs of larger basal ones. In older teeth the edges are worn almost smooth. First lateral broad, with short broad basal plate and the usual pattern of short denticles. Cusps lengthening and narrowing to about the 17th tooth, then shortening. All the laterals denticulate, the three to four outermost teeth slender and degenerate.

Caecum small, just breaking surface on the digestive gland and lying flat.

Cerebral ganglia fused. Visceral ganglia distinct in young specimens, fused in the adult, with large granular nerve cells.

SPECIFIC CHARACTERS

Medium size; green or brown colour, with numerous small, discrete, regular rings on the head and body; foot strong with pointed tail; penis short and broad, with a lobe at the base; parapodia free; opaline gland partly simple, partly compound, multiporous; shell with firm calcareous lining; closed mantle papilla; purple glands; radula with denticulations on the long narrow cusps of the laterals.

Indian Ocean and North-west Pacific.

References (see also synonyms)

Baba, 1949 : 25, pl. 4, as *hirasei*.
Baba, Hamatani & Hisai, 1956 : 216, as *hirasei* (breeding habits).
Eales, 1944 : 4, juvenile specimen.
Macnae, 1957 : 290.
Pilsbry, 1895 : 110 and 109 (*nodifera*), both as *Tethys*.

Aplysia (Varria) pulmonica Gould, 1852 : 223

Text-fig. 31

SYNONYMY : *Tethys pulmonica* Pilsbry, 1895 : 96.
T.p. var. *tryoniana* Pilsbry, l. c.

DISTRIBUTION. South-east Asia, islands in the South Pacific (Samoa, Hawaii, etc) and Australia.

MATERIAL EXAMINED. Specimens from Cochin China, Hawaii and other Pacific Islands.

The species was named by Gould from specimens collected at Samoa by the United States Exploring Expedition in the Pacific 1838–42. Pilsbry (1895) copied Gould's figure (pl. 18) as *Tethys* and added a variety *tryoniana*.

Aplysias of moderate size, up to 150 mm. long when alive and about 85 mm. long, 35 mm. wide and 49 mm. high when preserved. Rather broad and flat, almost oblong in shape. Skin moderately soft, not flabby, but may become nodular and like crocodile-skin in contraction, and may have calcareous granules embedded in it. Much black pigment is present, forming a reticulate pattern or lines, but the general colour is a dark bronze green, which dissolves out on preservation, leaving only the black pigment. Foot dark and may be speckled. Inner sides of the parapodia with dark and clear blotches, especially near the edges (Text-fig. 31*a*). On the back, between the anterior ends of the parapodia, the pigment may be arranged in longitudinal lines or bands. Mantle blotched all over with black, including the anal spout, sometimes with light round spots about 2 mm. in diameter, filled in with black between the spots. Mantle cavity floor and ctenidium lightly pigmented or pale. A specimen from Honolulu, collected by Dr. T. Mortensen with a normal specimen, was intensely black ; it is now in the University Museum in Copenhagen.

Head broad and flat, neck short and thick. Cephalic tentacles short, rolled, sometimes separated dorsally by a median groove, giving the head a bilobed appearance, with large mouth flaps. Eyes small. Rhinophores close to the cephalic tentacles, short and stout, close together, strongly contractile, resembling those of *dactylomela*. Gould described them as " faintly ringed ", but this was probably due to contraction.

Foot of moderate breadth, with rounded anterior edges, defined border and distinct pointed tail, tough and hard in contraction. Penis sheath small and not very muscular, with two small retractor muscles. Penis (Text-fig. 31*b*) broad, flat, curved and acuminate, the sperm groove reaching its tip. Parapodia widely spaced anteriorly, of moderate size, commencing close behind the rhinophores, joined low down posteriorly forming a small platform, or sometimes a low wall shutting in the mantle cavity. The dorsal area is fully exposed.

Mantle of moderate size, with a small tubular foramen on a ringed papilla, with or without starry rays. Anal siphon small, tubular, frilled. Purple glands present.

Mantle cavity not large. Opaline gland compound, with a large aperture, surrounded by numerous small openings. Genital aperture smooth edged, genital duct not raised on the floor of the mantle cavity, genital groove well marked.

Shell (Text-fig. 31*c*) oval, thick and flat. Horny and calcareous layers present, the deep yellow horny portion with strongly marked concentric lines. Apex oblique, without spire, but turned downwards, together with the ventral border of the short, deep anal sinus.

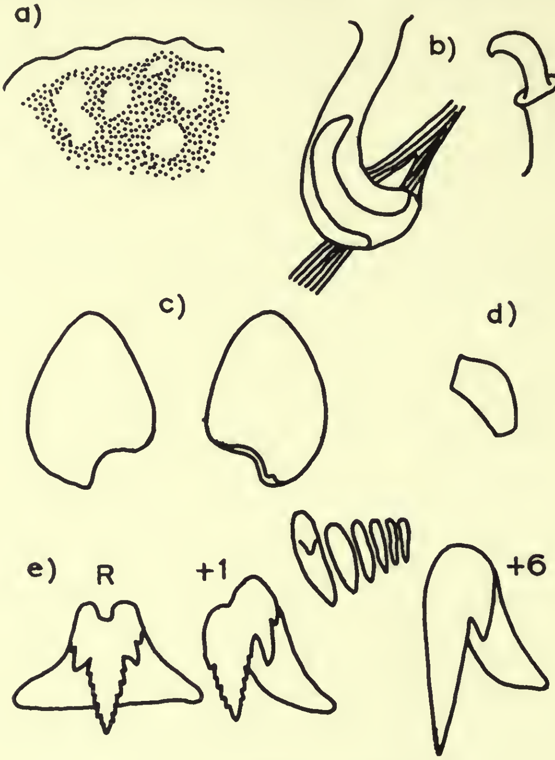

FIG. 31. *Aplysia pulmonica.*

(*a*) Inner side of parapodium to show light and dark areas and clear edges. (cf. *dactylomela*, which has branched vertical bands, Frontispiece.)
(*b*) Penis in its sheath and partly everted. × 2½.
(*c*) Shell in dorsal and ventral views. Note the almost pointed anterior border. × ⅔.
(*d*) Jaw plate (cf. *dactylomela*, Fig. 7*f*).
(*e*) Radular teeth. Rhachidian, first, sixth and outermost lateral teeth. × 80.

Jaws (Text-fig. 31*d*) rounded with short, rather broad rods, some serrated on their free edges.

Radula (Text-fig. 31*e*) with about 60 rows and a formula up to 50.1.50. Rhachidian tooth with short but broad basal plate, slightly excavated posteriorly and deeply so anteriorly. Cusp longer than the plate in young teeth, with fine denticles which wear down in older teeth, and a rather large basal denticle on each side, which may become subdivided. First lateral with short squat plate, finely denticulate broad cusp and the usual large basal denticle laterally. Remaining laterals with straight cusps of increasing length up to the middle of the row, almost smooth, with stout blunt basal denticle. Outermost three to five teeth vestigial.

Caecum inflated at the tip, recurved or straight.

Cerebral ganglia band-like, visceral ganglia joined but not completely fused.

Specific Characters

Moderate size, low broad shape, reticulate skin pattern, broad or moderately broad foot with pointed tail, broad flat penis, small parapodia joined low down, tubular foramen with starry rays in mantle, compound opaline gland with large aperture surrounded by small separate openings, broad oval shell with oblique apex, simple radula, the outer laterals almost smooth and spiky.

Western Pacific from Asia to Australia.

Note. Some specimens in contraction have a resemblance to *A. dactylomela*, but are lower and flatter, without rings on the skin, with a circlet of apertures to the opaline gland in addition to the main aperture, with a differently shaped penis, jaw plate, etc. *Pulmonica* and *dactylomela* occur in the same region in Honolulu and can be readily distinguished. Farran (1905 : 349) suggested that *pulmonica* and *cornigera* might be the same species. For differences between the two species see p. 303.

Aplysia (Varria) rehderi sp. nov.

Text-figs. 32 and 33

Distribution. Monterey, California, U.S.A.

Material examined. A single specimen in the U.S. National Museum (The Smithsonian Institution), Washington, U.S.A. The species is named in honour of Dr. Harald Rehder, Curator of Mollusks, U.S. National Museum. Holotype U.S.N.M. 575055.

The specimen measures 116 mm. long, 40 mm. wide and 62 mm. high, and is therefore of moderate size. There is little trace of colour, mostly black pigment on the inner sides of the parapodia. Skin thick and rather tough, probably much contracted. The general shape is low and rounded (Text-fig. 32, *a*, *b*).

Head rather large and low, the neck narrower than the head. Cephalic tentacles (Text-fig. 32*c*) short and ear-like, free from the mouth slit. Eyes minute. Rhinophores slender, tapering, fairly close together.

Foot narrow, thick, smooth, 28 mm. broad at the broadest part, rounded in front, prolonged into a well developed pointed tail, projecting 12 mm. behind. Penis (Text-fig. 32*d*) enormous, thick at the base, at least 36 mm. long, spirally twisted, narrowing at the apex, the groove extending to its tip. Genital groove deep on the penis itself and on the muscular part of the stout, thick-walled sheath, the distal (bulbous) part of which is relatively small and smooth-lined. Parapodia small, tight, arising 16 mm. apart, not very high, joined behind, forming a low wall about 8 mm. high around the mantle cavity. They are probably much contracted.

Mantle long and narrow, 57 × 22 mm., thin, with a papilla at the point of closure, a good overhang anteriorly, but not much over the ctenidium. Anal spout short, broad, with sinuous margin. It is not possible to determine the colour of the secretion of the mantle glands.

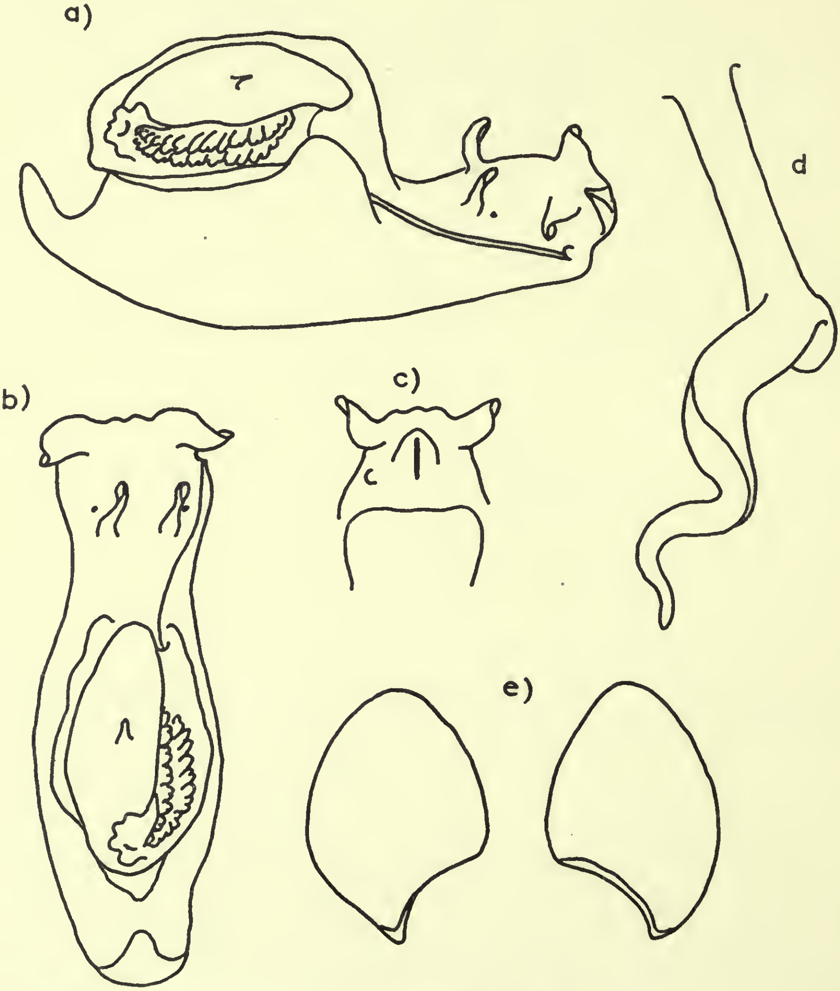

FIG. 32. *Aplysia rehderi.*

(*a*) Lateral view. $\times \frac{2}{3}$.
(*b*) Dorsal view. Note the narrowed neck region. $\times \frac{2}{3}$.
(*c*) Head in ventral view.
(*d*) Penis and penis sheath. × 1.
(*e*) Shell in dorsal and ventral views. $\times \frac{2}{3}$.

Mantle cavity not large. Ctenidium very large and thick, 34 × 16 mm., curved round into the anal siphon. Opaline gland of medium size, compound, uniporous. Genital aperture very large and swollen, smooth, hardly covered by the mantle, genital groove deep.

Shell (Text-fig. 32*e*) 46 × 33 mm., broadly ovate, shallow, of unusual shape owing to the extreme narrowing at the apex. Horny and calcareous parts present, the former delicate with concentric ridges. No spire. Anal sinus long and deep.

Jaws large and rectangular. Rods long, packed tightly together, rounded at the tips.

Buccal mass very large, the radula (Text-fig. 33) being the largest of any species examined. It was 15 mm. long and 15 mm. broad, with 70 rows and a formula 56.1.56. Rhachidian tooth with a short broad basal plate, rather shapeless and not incised, the cusp broad, shorter than the base, with a few indistinct denticles and broad denticulate basal denticle. First lateral short and broad, with curved basal plate and broad cusp shorter than the plate, its denticles small and fine. The cusps get narrower and longer along the row, and are almost straight down from the head, which is swollen and high. Denticles fine near the tip, mesially a few irregular ones and laterally large curved prongs, three to five in number, or even more, the most distal nearest the tip the longest, but very variable and irregular. The outer laterals with slender narrow plates and shorter cusps. Up to three vestigial teeth at the end of the row.

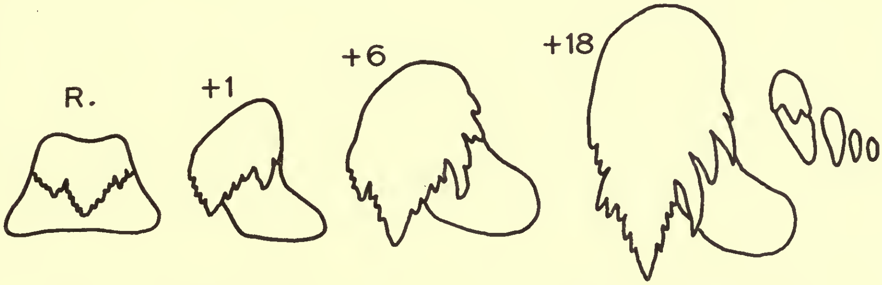

FIG. 33. *Aplysia rehderi*. Radular teeth. Rhachidian, first, sixth, 18th and outermost lateral teeth. × 80.

Cerebral ganglia fused to form a band.

SPECIFIC CHARACTERS

Thick skinned, with swollen head owing to the large size of the buccal mass and the penis. Foot narrow, shorter anteriorly than the head, prolonged posteriorly into a pointed tail. Parapodia thick, joined posteriorly to form a low wall around the mantle cavity. Mantle thin, with conical papilla. Ctenidium large ; opaline gland compound, uniporous ; genital aperture and duct exceptionally large. Shell broadly ovate, shallow ; apex narrow, without spire or " accessory plate "; anal sinus long and deep. Radula 70 × 56.1.56, very large and broad, simple in the rhachidian and first few lateral teeth, then becoming elaborate in denticulation. Penis very large and stout, spirally twisted, narrowed at the apex ; penis sheath smooth-lined distally.

California.

Aplysia (Varria) reticulata sp. nov.

Text-fig. 34

DISTRIBUTION. North-west Australia, Queensland, Dampier Archipelago.

MATERIAL EXAMINED. Five specimens from these areas, three from Queensland in the Australian Museum at Sydney, two in the British Museum. Type B.M. (N.H.), 86.2.22.29 from N.W. Australia.

Rather small Aplysias, the larger of the British Museum specimens measuring 44 mm. long, 25 mm. broad and 29 mm. high when contracted. Skin firm and wrinkled, dirty yellow, with solid black spots scattered on the sides, and branched and anastomosing bands of dark pigment on the inner faces of the parapodia. Mantle roof in all the specimens with small black spots linked by less dense black anastomosing lines forming a network (Text-fig. 34, *a–d*).

Head and neck small but contracted. Cephalic tentacles continued to the sides of the mouth slit. Rhinophores close together, stout, not as close together as in *A. sydneyensis*.

Foot narrow, only 10 mm. wide, very muscular and tough, with a short pointed tail. Penis (Text-fig. 34*e*) short, flat, moderately broad, tapering. Parapodia large, arising close together far forwards on the neck and rising high above the mantle, then sloping towards the tail, but hardly joining posteriorly low down. The edges are fimbriated and thin.

Mantle rather small and thick, 27 × 15 mm. There is a minute aperture in one specimen, but in another the shell sac is closed. Anal siphon of moderate size, frilled, projecting backwards between the parapodial lobes. Purple glands are present.

Mantle cavity large and open. Opaline gland simple, multiporous. Genital aperture not enlarged, crescentic.

Shell (Text-fig. 34*f*) 24 × 17 mm., delicate, with broken calcareous lining, elongated oval in shape, without distinct spire, deeply concave ; anal sinus wide but not deep.

Jaws with very long, light brown, curved rods, closely packed together.

Buccal mass small. Radula (Text-fig. 34*g*) 8 × 5 mm., rather narrow ; 50 rows, 25.1.25. Rhachidian tooth with broad basal plate, slightly excavated on the posterior border and deeply so anteriorly. Cusp broad and blunt, almost as long as the base, with weak denticles. Laterals with short, rather square bases and more deeply cut denticles. One mesial denticle and two lateral denticles are larger than the others. Outermost two or three teeth degenerate. A common type of radula.

Caecum curved and inflated at the tip.

Cerebral ganglia fused, visceral ganglia joined.

Specific Characters

Small size, spotted skin, reticulate pattern on the mantle roof, narrow foot with short tail, short flat penis, high free parapodia, minute mantle aperture or none, purple glands, simple multiporous opaline gland, deeply concave delicate shell, chief ganglia joined.

Australia.

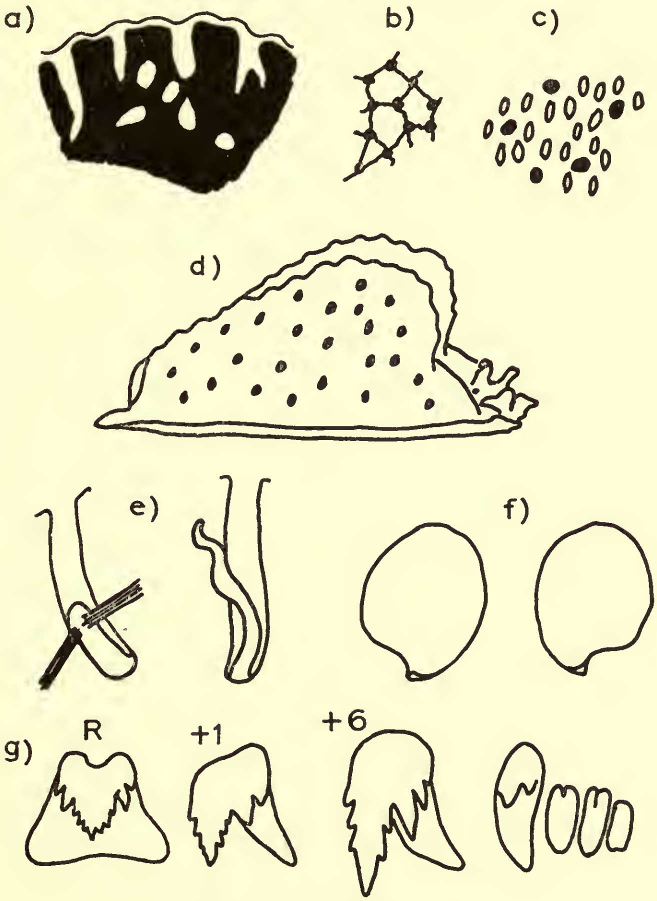

FIG. 34. *Aplysia reticulata.*

(*a*) Pattern on the inner side of the parapodium. Edge light, then vertical alternating bands of light and dark, with light blotches.

(*b*) Pattern on the mantle roof. Reticulate black lines with enlargements at the junctions.

(*c*) Pattern on the side of the body. Oval or round black spots, interspersed with more numerous light areas on a dull yellow ground.

(*d*) Specimen from the Dampier Archipelago, Australia, in lateral view. × $\frac{2}{3}$.

(*e*) Penis sheath and its retractors, and sheath opened and extended to show the penis. × 2.

(*f*) Shell in ventral and dorsal views. × $\frac{2}{3}$.

(*g*) Radular teeth. Rhachidian, first, sixth and outermost lateral teeth. × 80.

Aplysia (Varria) robertsi Pilsbry, 1895 : 89, pl. 55 (as *Tethys*)

Distribution. West coast of North America, from Mexico to Central America.

Material examined. One specimen from the west coast of Central America, now in the British Museum (Natural History).

Of moderate size, about 110 mm. preserved, the B.M. (N.H.) specimen being 93 mm. long, 35 mm. wide and 44 mm. high. Slender, soft and flabby. Pilsbry describes the colour as dirty light olive, with black-brown reticulations on both sides of the parapodia. Foot sole black. Mantle clear olive, the free border and siphon black. The specimen examined had the remains of black vertical stripes on the inner faces of the parapodia, and there was black pigment on the mantle roof and ctenidium, but not on the mantle floor.

Head and neck elongated, the neck wider than the narrow head. Cephalic tentacles very small, slightly rolled on the edges. Rhinophores contracted, but thick, close together and set far back. Eyes plainly visible, antero-lateral to the rhinophores.

Foot wide accordingly to Pilsbry, but strongly contractile and may appear narrow. Soft and fleshy, not strongly muscular. Tail long and slender. Penis sheath small, with a single retractor muscle, smooth-lined in the portion near the attachment of the small, flat, pointed penis. Parapodia rounded, thin, sinuous on the margins, arising far back, spreading widely, and meeting, but not joining low down posteriorly over the foot, forming an extension of the mantle cavity floor, which is not quite flat.

Mantle 38 × 24 mm. in the 93 mm. specimen, with a minute papilla at its point of closure over the shell. Anal siphon broad and high. Purple glands present.

Mantle cavity exposed. Opaline gland small, compound, with a single crescent-shaped aperture. Genital aperture not inflated, smooth edged.

Shell delicate, thin and fragile, oval, almost flat ; 35 × 28 mm. Apex weak, with narrow, reflexed margin, anal sinus long and shallow (Pilsbry, 1895 : pl. 55, fig. 5).

Radula 7 × 5 mm., flat, with 47 rows and formula 28.1.28. Narrower and less pointed than that of *brasiliana*. Rhachidian tooth with moderate, rather high basal plate, straight posterior border, short cusp a little longer than the plate, with well marked denticles, the basal denticle pronounced as usual. First lateral with short straight plate, short broad cusp and sharp denticles. Other laterals with longer cusps and elaboration of the denticles, all of which are deeply cut. Three to four vestigial teeth at each end of the row.

Caecum small and appearing flat on the surface of the digestive gland.

Cerebral ganglia fused, visceral distinct.

Specific Characters

Moderate size, slender flabby body, short cephalic tentacles, long tail, fleshy foot, freely mobile, thin parapodia, minute mantle papilla, small compound opaline gland with one aperture, oval delicate shell, strongly denticulate radula, short flat pointed penis.

West coast of North and Central America.

The species bears considerable resemblance to *A. brasiliana*, but differs in the small size of the cephalic tentacles and the opaline gland, the shape of the genital duct beneath the mantle floor, the narrower radula with its more deeply cut denticulations, and the shape of the short, flat pointed penis. Pilsbry's specific name has therefore been retained until more information and specimens are available.

Aplysia (Varria) sagamiana Baba, 1949 : 26, pl. 4

Text-fig. 35

DISTRIBUTION. Japan.

MATERIAL EXAMINED. Seven specimens from the Naturhistoriska Riksmuseum, Stockholm, collected by Dr. T. Gislén's Pacific Expedition, 1930–31, at Misaki, Sagami Bay, in 2–3 fm., on *Zostera*.

This pretty little Aplysia was first taken by His Imperial Majesty the Emperor of Japan and named and figured in colour by Baba, who also sketched the shell and radula.

The largest Swedish specimen measures 31 mm. long, 10 mm. wide and 16 mm. high. Baba gives 70 mm. as a typical length, so that all specimens are small. Alive they are pinkish red in colour, with black spots on the head, neck, sides and parapodia. These spots are small, and may have the appearance of interrupted black margins to the parts concerned, distinguishing the species from *A. parvula*, in which the margins are continuous. The cephalic tentacles and rhinophores are tipped with black, the mantle is mottled. The general shape is slender, high and narrow, the skin soft.

Head small, neck long. Cephalic tentacles wide, slender, rolled on the edges, fluted in some specimens, continued to the ventral sides of the mouth slit. Eyes plain but small, close to the base of the rhinophores, which are small, slender, acutely pointed and slit as usual.

Foot narrow, only 6 mm. wide in a 27 mm. specimen, soft, rounded in front, a little wider at the middle, with narrow pointed tail and the edges plainly marked against the pigmentation of the sides of the body, for the foot is colourless. Penis (Text-fig. 35*b*) of the short, broad type, in a smooth-lined and not enlarged sheath. Parapodia well developed, rounded, with fluted margins, the inner sides with a block pattern of dark and light areas (Text-fig. 35*a*), capable of closing over the dorsal region or of spreading wide open, joined low down on the foot posteriorly, forming a flat continuation of the mantle cavity floor.

Mantle 12 × 8 mm., soft and thin, with a small flat aperture, rayed. Siphon rounded and low. Purple secretion exuded.

Mantle cavity of moderate size, open at both ends. Ctenidium small and neat, opaline gland small, simple, multiporous, but there is a tendency for the anterior vesicles to be grouped and for their ducts to join to form a larger aperture than the others. Genital aperture under cover of the mantle rim, genital groove small.

Shell elongated, oval, 10 × 7 × 2 mm., not strongly concave, delicate, without spire, apex acute, oblique, edge slightly recurved ; anal sinus well formed.

Jaws composed of flat-topped rods, often with a little projection at one corner.

Radula (Text-fig. 35*d*) 29 × 18.1.18, but Baba gives 35 × 22.1.22. Rhachidian tooth with short but broad basal plate, the anterior border unusually broad and deeply incised. Cusp as long as or slightly longer than the base, with about seven neat graduated denticles on each side, the basal ones being large. In older teeth the fine denticles are worn down, but the basal denticles become accentuated. First lateral with a bulbous head and short tapering basal plate, the denticulations resembling those of the rhachidian, but the mesial basal denticle is smaller. Along the row the basal plates become elongated and curved, the head narrows, the cusp elongates and so does the penultimate lateral denticle. After the middle of the row the cusps shorten and eventually disappear, until the three to five outermost vestigial teeth are reached. This is a neat, well denticulated radula.

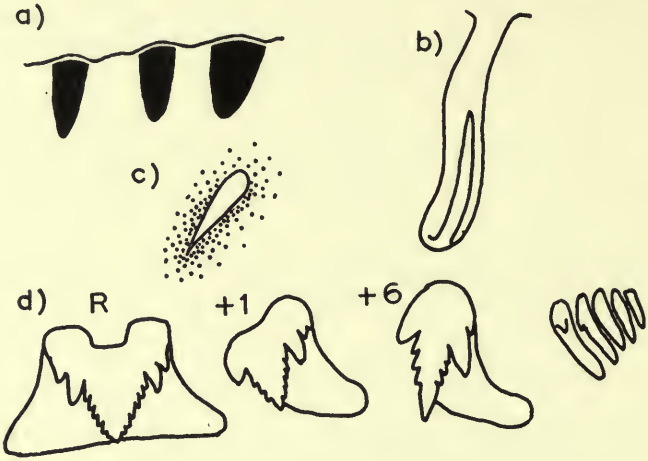

FIG. 35. *Aplysia sagamiana.*

(*a*) Block pattern on inner side of a parapodium.
(*b*) Penis in its sheath. × 10.
(*c*) Caecum exposed on the surface of the digestive gland and lying flat.
(*d*) Radular teeth. Rhachidian, first, sixth and outermost lateral teeth. × 132.

Caecum lies flat on the surface and is somewhat inflated at the apex (Text-fig. 35*c*).

All the nerve ganglia are distinct and separate, but the cerebral ganglia are contiguous, without a visible commissure.

SPECIFIC CHARACTERS

Small, with interrupted or speckled black markings on a pinkish red ground ; long cephalic tentacles, narrow foot and slender tail ; short broad penis ; relatively large parapodia, fluted at the edges, mobile, joined low down on the foot posteriorly. Mantle thin, with a small flat rayed aperture. Purple secretion. Opaline gland simple, multiporous, but with a tendency to fusion of the anterior vesicles. Shell delicate, shallow, with acute oblique apex. Radula small, up to 35 rows and formula 22.1.22, rhachidian tooth broad, deeply incised anteriorly, with clear cut and regular denticles, laterals also with neat graded denticles. All the nerve ganglia distinct.

Japan.

There is some resemblance between this species and *A. parvula*, but the pattern and markings, the low junction of the parapodia, the small mantle aperture, the shallow shell without spire and the broad rhachidian tooth of the radula distinguish it. One resemblance, however, is in the primitive separation of the chief nerve ganglia, so that this species forms a link between the subgenus *Pruvotaplysia* and the main group in which the cerebral ganglia are fused.

Aplysia (Varria) sowerbyi Pilsbry, 1895 : 101

Text-fig. 36

SYNONYMY: *A. tigrina* (*non* Rang, 1828) ; Angas, 1867 : 228 ; Sowerby, 1869, pl. 2.

DISTRIBUTION. Australia, New South Wales. Victoria.

MATERIAL EXAMINED. Four specimens from Long Reef, Sydney, New South Wales, October 1957, E. Pope and party.

The four specimens are small, the largest being 67 mm. long, 16 mm. wide and 27 mm. high, with parapodia spread 38 mm. wide, foot 12 mm. wide. They bear a general resemblance to *sydneyensis* in their slight build. Colour yellowish green with small dark brown blotches, or dark greenish brown with light, almost white, spots and faint brown markings. There is an all-over brownish black reticulation, either making a honeycomb pattern or drawn out near the edges of the parapodia into parallel vertical lines. The preserved specimens have neither colour nor markings on the foot, inner sides of the parapodia, mantle, or mantle cavity floor, except for a tinge of grey over the opaline gland. Skin soft and flabby.

Head small, with short neck (Text-fig. 36*b*). Cephalic tentacles small, curved backwards, almost sickle shaped, with small connections with the sides of the mouth ; the shape is characteristic. Eyes large and conspicuous. Rhinophores very long (12 mm.), set very close together, slit deeply.

Foot narrow, soft, with rounded anterior edges, not well marked off laterally from the sides of the body, posteriorly with a short triangular tail about 5 mm. long. Penis sheath small, recurved; with two small retractor muscles (Text-fig. 36*d*). Penis filiform, small (Text-fig. 36*e*). Parapodia not large, soft and thin, mobile, arising close to the rhinophores, rounded, with slightly sinuous edges. Posteriorly they do not unite or meet, but stand up like the edges of a rounded collar, with about 3 mm. space between them, the mantle cavity being therefore open posteriorly.

Mantle thin, narrow, pointed anteriorly, with a thin flap laterally where a purple gland lies, and a soft, broad, rounded anal spout, which in one specimen is expanded and leaf-like. There is a minute papilla at the point of closure over the shell, probably open during life.

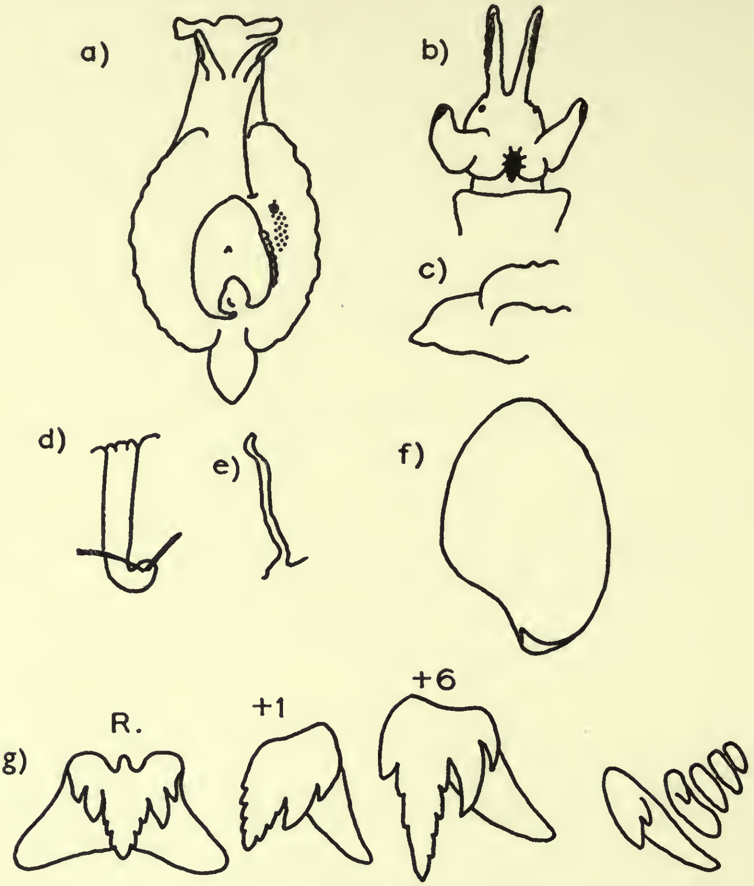

FIG. 36. *Aplysia sowerbyi.*

(*a*) Dorsal view of specimen with expanded parapodia. × ⅔.
(*b*) Head of another specimen in anterior view. × 1½.
(*c*) Tail in lateral view to show upstanding parapodia, which do not join or meet. × 1½.
(*d*) Penis sheath and its two weak retractor muscles. × 1½.
(*e*) Penis. × 2.
(*f*) Shell in ventral view. × 1½.
(*g*) Radular teeth. Rhachidian, first, sixth and outermost lateral teeth. × 132.

Mantle cavity open at both ends. Genital aperture small, smooth, not inflated, inconspicuous. Opaline gland large, reniform, slightly pigmented, with one larger and numerous small apertures of the predominantly simple gland. Ctenidium small, unpigmented.

Shell (22 × 16 mm.) as figured by Sowerby and copied by Pilsbry (Text-fig. 36*f*). It is firm and horn coloured, with distinct growth rings in the form of ridges. Shape narrow and concave, with dense but smaller calcareous lining and a hard, strongly calcified and oblique, incurved apex. It is unlike the delicate shell of *sydneyensis* or the almost flat shell of *cronullae*.

Jaws 4 × 3 mm., curved, brown. Rods long, almost straight, rounder and a little wider at the tip.

Radula 7 × 5 mm., with about 45 rows and formula 26.1.26 (Text-fig. 36*g*). Rhachidian tooth with broad basal plate, slightly excavated posteriorly and incised anteriorly but with a small projection centrally. Cusp about equal in length to the plate, strong, with well marked and rounded denticles, the two basal ones of each side being enlarged. First lateral with a narrow triangular basal plate, broad head and short cusp, the denticles repeating those of the rhachidian tooth. Along the row the basal plates elongate and become curved, but not very broad, the cusps lengthen and are narrow and spiky, longer than the plates. Their denticles are weak near the apex, but there is one strong mesial denticle and laterally there are at least three, of which that nearest the apex is the largest and may be nearly half the length of the cusp, giving a two-pronged appearance to the teeth. From three to four of the outermost teeth are small and vestigial.

Caecum appearing flat on the surface of the digestive gland.

Cerebral ganglia fused, flat, band-like ; visceral ganglia distinct.

Specific Characters

Medium size, slightly built. Ground colour yellowish green to dark brownish green, with small dark blotches, sometimes light spots and usually with dark reticulations. Pale on the foot, inner sides of the parapodia, mantle and lining of the mantle cavity. Skin soft. Head small, neck short. Cephalic tentacles short, sickle-shaped. Rhinophores long, deeply slit, set very close together. Foot narrow, with short tail. Penis small, filiform, in a small, recurved sheath. Parapodia thin, mobile, not joining or meeting posteriorly. Mantle thin, with minute papilla. Purple glands present. Mantle cavity open at both ends. Opaline gland large, reniform, simple, with one large and numerous small apertures. Shell firm, concave, with strongly oblique hard apex. Radula 45 × 26.1.26, characterized by long spiky cusps of the laterals and narrow basal plates.

Australia, New South Wales.

The species is related to *sydneyensis* and *cronullae*. It resembles the former in its slight build, small head and cephalic tentacles, narrow foot, filiform penis, weak parapodia, simple multiporous opaline gland and radular formula. Its resemblances to *cronullae* are the filiform penis, large opaline gland, small mantle papilla and radular formula. It differs from both in the absence of pigment on foot, inner sides of the parapodia, mantle and mantle cavity floor, in the fusion of some of the opaline glands to discharge by a larger anterior aperture than the small ones of the isolated gland cells, in the hard oblique apex of the firm, concave shell and the long spiky lateral radular teeth.

Aplysia (Varria) sydneyensis Sowerby, 1869 : pl. 7

Text-fig. 37

SYNONYM : *A. excavata* Sowerby, 1869 : pl. 3.

DISTRIBUTION. Australia : New South Wales, Victoria, South Australia, Western Australia, Queensland.

MATERIAL EXAMINED. Specimens from all the above areas.

This species was named by Sowerby from a shell, and has never been clearly defined. Australian zoologists recognize the species, and this account is based on specimens named by them in their museums.

Aplysias of moderate size, usually about 125 mm. long, shrinking to 80 mm. long, 22 mm. wide and 28 mm. high when preserved. Rather low in shape and not bulky (Text-fig. 37, *a*, *b*). Colour dark brown to almost black, spotted all over with cream, grey or dark brown spots, with a black lined pattern on the head and sides, reticulate in places. The mantle has a characteristic pattern of dark dots scattered on a light ground and forming rings at intervals, or radiating stripes (contrast *A. reticulata* p. 340). Foot dark. Inner sides of the parapodia with black bands arranged vertically and lighter spots near the edges. No pigment on the ctenidium or the mantle cavity floor. Skin soft, wrinkled.

Head small, neck short and thick. Cephalic tentacles short, pointed, rolled on the edges, not projecting much. Eyes small. Rhinophores tall, tapering and slender, very close together.

Foot narrow to moderate, contracting with irregular wrinkles, soft and flabby, anterior edges rounded, tail distinct, slender. Penis sheath small, penis short but narrow and pointed (Text-fig. 37*c*). Parapodia mobile, not large, commencing close to the rhinophores, rounded at first, thin, their edges sinuous but not fimbriated, meeting low down over the foot posteriorly, forming a platform-like extension of the mantle cavity floor. The dorsal area is fully exposed.

Mantle rather small, long and narrow, thin, with an aperture about 1 mm. in diameter marked by black radiating lines, but in a much contracted specimen this may be reduced to a small papilla. Anal siphon tubular, rounded, or tall and leaf-like. Purple glands present.

Mantle cavity widely open. Ctenidium of moderate size. Opaline gland small, pyriform, simple, multiporous. Genital aperture small, crescentic, covered by the mantle edge, genital groove delicate.

Shell (Text-fig. 37*d*) thin, pale in colour, narrowly oval and concave, with horny and calcareous matter, and an anal sinus, which is very short, posteriorly placed and shallow. Apex narrow and hard, lines of growth pronounced.

Jaws dark brown, almost triangular in shape. Rods short to moderate, curved at the tip, tapering.

Buccal mass small, radula acutely pointed, 7 × 7 mm. (Text-fig. 37*e*). Formula about 45 × 28.1.28 but usually less. All the teeth except the outermost vestigial ones denticulate, with rather short basal plates and heavily built heads. Rhachidian tooth sunken and pale, with a short and moderately broad shouldered basal plate, excavated anteriorly and almost straight posteriorly, the cusp shorter than the plate and bearing feeble denticles, of which the basal pair are usually larger than the others. The first lateral also has irregular denticles on a short cusp, a broad head and out-turned basal plate. Further along the row the cusps remain broad but do not increase greatly in size, although their plates become narrower. The mesial basal denticles tend to form a projecting ridge on the edge of the cusp and the lateral basal denticles are enlarged and may be secondarily denticulate. The outermost three teeth are vestigial.

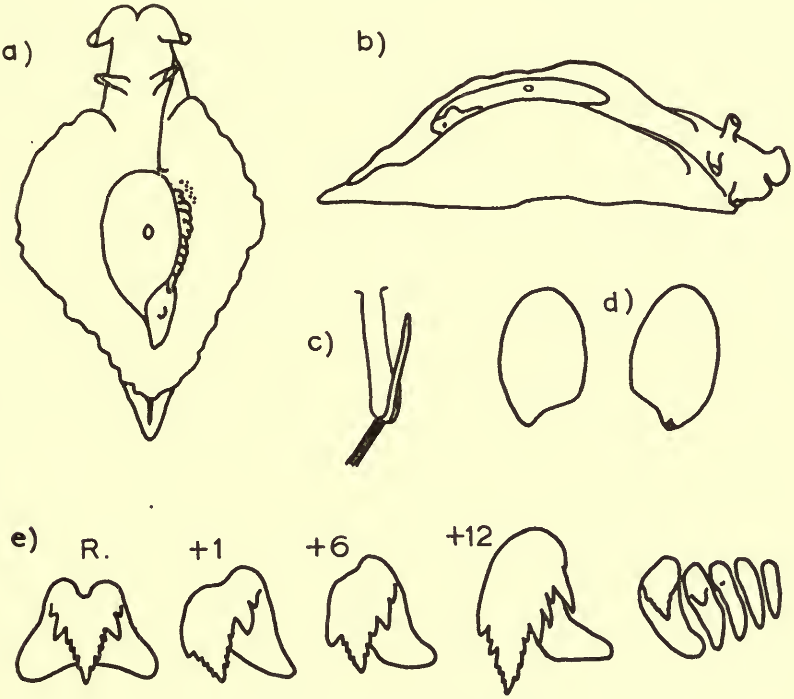

FIG. 37. *Aplysia sydneyensis.*

(*a*) Dorsal view of a specimen with expanded parapodia. × $\frac{2}{3}$.
(*b*) Lateral view of another specimen. × $\frac{2}{3}$.
(*c*) Penis sheath opened to show the narrow penis. × $1\frac{2}{3}$.
(*d*) Shell in dorsal and ventral views. The fine concentric ridges are not shown. × $\frac{2}{3}$.
(*e*) Radular teeth. Rhachidian, first, sixth, 12th and outermost lateral teeth. × 80.

Caecum straight, just reaching the surface of the digestive gland near its tip.

Cerebral ganglia fused, visceral still separately recognizable.

SPECIFIC CHARACTERS

Moderate size, low shape, pattern of lines and spots, small head and short cephalic tentacles, narrow foot with slender tail, short narrow pointed penis, mobile parapodia fused low down on the tail, flat mantle aperture with radiating lines, simple opaline gland with many apertures, oval hyaline concave shell with shallow anal sinus, radula with few teeth in a row, short bases, enlarged heads and irregular denticles.

Australia.

The copepod *Strongylopleura pruvoti* Monod & Dolfuss, 1932 was found in the mantle cavity of three specimens from Sydney, now in the Naturhistorisches Museum, Wien. See also p. 368.

References (*see also synonym*)

Allan, 1932*a* : 419 ; 1950 : 213.
Angas, 1877 : 190, as *sydneyensis* and *excavata.*
Hedley, 1918 : 107, as *Tethys sydneyensis* and *excavata.*
Hutton, 1882 : 118.
Pilsbry, 1895 : 100, as *T. excavata* ; 101, as *T. sydneyensis.*

Aplysia (Varria) willcoxi Heilprin, 1886 : 364

Text-fig. 38

SYNONYM : *Tethys willcoxi* var. *perviridis* Pilsbry, 1895 : 81.

DISTRIBUTION. East coast of North America, from New England to the West Indies. Recorded from Woods Hole, Mass.; New Jersey ; Rhode Island ; Dry Tortugas ; Florida and Guadeloupe.

MATERIAL EXAMINED. Specimens from Woods Hole and Fisher Island, New York.

First recorded by Heilprin from Florida, this species is now the most northerly one known on the East Atlantic coast of North America. It is a large, very bulky Aplysia, about 200 mm. long, but contracting considerably when preserved (Text-fig. 38*a*). A specimen from Fisher Island measured 110 mm. long, 40 mm. wide and 54 mm. high. Skin smooth but tough and leathery. Colour variable, greenish yellow ground colour with irregular purplish black marbling on the parapodia, neck and head, sometimes with round dark spots or blotches and light areas on the inner sides of the parapodia, but these are not regular. Foot, mantle and ctenidium dark. Plain deep seagreen specimens were described as var. *perviridis*. Green specimens may have a reticulate black pattern with some white spots. When preserved the markings are obliterated and much green pigment is exuded into the preserving fluid, the whole animal appearing deep green in colour. Sanford (1922) states that the animal has " a slightly unpleasant odour ".

Head and neck large. Cephalic tentacles well developed, broad, curved, rolled at the edges. Rhinophores set well back and fairly close together, conical, with short slits.

Foot narrow, 30 mm. wide anteriorly, narrowing to 25 mm. Front edges rounded, sides ill defined, tail short. Penis very long, filiform, 45 mm. long in the 110 mm. specimen. (Pilsbry gives a figure of a penis only partly extruded from its sheath and describes the latter as the penis itself.) Parapodia large, thick, natatory, arising close to the rhinophores, borders smooth or slightly irregular but not fimbriated, joined low down over the foot.

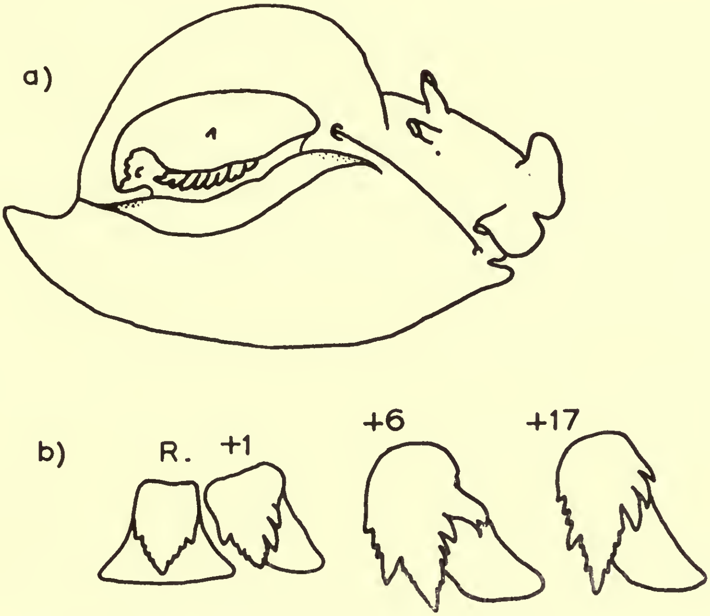

Fig. 38. *Aplysia willcoxi* var. *perviridis*.

(*a*) Lateral view. × $\frac{2}{3}$.
(*b*) Radular teeth. Rhachidian, first sixth and 17th lateral teeth. × 80.

Mantle large with minute tubular foramen, sometimes surrounded by wrinkles or short black radiating lines. Anal siphon long, wide and tongue-like, but contractile. Purple glands exude a reddish purple fluid which turns crimson in formalin.

Mantle cavity with large ctenidium, compound uniporous opaline gland and large inflated genital aperture with smooth edge.

Shell broad, flattened, thin, with some calcareous matter. It measured 56 × 43 mm. Concentric and radiating ridges marked, apex small, curved, anal sinus long but shallow, with a thickened reflected margin.

Jaws large, composed of closely packed, short, slightly curved rods.

Radula (Text-fig. 38*b*) large, 11 × 10 mm. About 60 rows and a formula of 30.1.30. Rhachidian tooth feeble, lighter than the other teeth, the basal plate rather long, with straight anterior and posterior borders and short rounded cusp, bearing weak denticles, the basal one, as usual, larger than the others. First lateral with short basal plate, large head and short cusp, upon which the median basal denticle is well developed, as well as two or three lateral ones, but the apical denticles are mere nodules. The basal plates of the remaining lateral teeth become squared off, but the cusps rarely exceed the plates in length. A striking feature of this radula is the elaboration of the basal denticles on each side of the cusp. Thus the 17th lateral has four well developed basal denticles mesially and three or four large ones laterally, although the denticles of the main cusp remain feeble. The three outermost teeth are vestigial.

Caecum small, only its tip appearing on the surface of the digestive gland.

Cerebral ganglia fused to form a flat band. Visceral ganglia joined but not fused.

SPECIFIC CHARACTERS

Large size, bulky shape, tough skin, dark colouring of all parts with abundance of deep green in the var. *perviridis*. Cephalic tentacles large, rhinophores close together, foot narrow, penis long, filiform, parapodia smooth, natatory, joined low down posteriorly, minute mantle foramen, purple glands, opaline gland compound uniporous, radula large with elaboration of the basal denticles.

North-west Atlantic.

References (*see also synonym*)

Merriman, 1937 : 95.
Sanford, 1922 : 80.
White, 1952 : 112.

Aplysia (Varria) winneba Eales, 1957 : 180

DISTRIBUTION. West coast of Africa : Ghana, near Accra ; Cape Verde Islands.

MATERIAL EXAMINED. Numerous specimens from this area. Colour photographs of the living animal swimming in a rock pool were lent by Mr. R. Bassindale, who collected many of the specimens.

Lectotype B.M. (N.H.), 1957.5.14.1. (Eales, 1957 *Proc. malac. Soc. Lond.* **32** : 208).

Aplysias of medium size, highly mobile, a typical specimen, preserved, measuring 70 mm. long, 55 mm. wide and 45 mm. high, being therefore broader than high when the parapodia are spread. When strongly contracted, however, the small head is drawn in, the parapodia are contracted tightly over the mantle but do not quite close the dorsal slit, and the inflated sides of the body make the animal appear like a little balloon. A large number of the specimens were in this condition. The general colour is purplish black, with browner shades on the mantle, vertical bars of black alternating with lighter areas on the inner edges of the parapodia, and a characteristic light triangular patch at the anterior end. When preserved the purple colour fades out, leaving a mottled pattern of grey and brownish black, with lighter areas between. There is no definite pattern and no rings are present. Some specimens have chalky granules embedded in the skin, which is soft and firm. The foot and mantle floor are unpigmented; the mantle may have radiating irregular lines or blotches of pigment.

Head and neck small, but the neck is long. Cephalic tentacles short and broad when contracted, but expanded they stand out from the sides of the head, and have fimbriated edges. They are linked with the ventral sides of the mouth slit. Eyes small. Rhinophores slender and pointed, strongly contractile, slit half-way down.

Foot of moderate width, about 20 mm. wide in a 90 mm. specimen. Tough and nodular in contraction, its borders defined and wavy. Tail short and tapering. Penis long and filiform, but can be inflated, penis sheath smooth lined. Parapodia not large, but strongly contractile. They arise by rounded edges rather far back, almost at the level of the genital aperture, and are spread wide in swimming, being flapped upwards alternately during this movement. They are joined low down over the tail, forming a kind of spout into which the anal siphon fits. Their edges are fimbriated.

Mantle of moderate size (26 × 19 mm. in a 70 mm. specimen), thin, with a small open tube about $\frac{1}{2}$ mm. in diameter. Anal siphon broad and frilled, with a tendency to form a spout towards the tail, or standing upright with reflexed edges. Purple glands present.

Mantle cavity shallow. Ctenidium colourless, of medium size. Opaline gland compound, large, with conspicuous aperture. Genital duct raised on the mantle cavity floor, its aperture fimbriated.

Shell 30 × 23 × 4 mm., of narrow oval shape, with remains of a calcareous layer. Apex without spire, but slightly recurved, and the dorsal side is turned back. Anal sinus rather long.

Jaws of slender, slightly curved rods, tightly and neatly packed.

Radula 8·5 × 7 mm., about 55 rows and a formula 37.1.37. The rhachidian tooth is high for its width, with a rounded cusp, irregularly denticulate. The first lateral has a similar rounded cusp, one larger denticle mesially and one laterally, in addition to those on the cusp itself. Along the row the cusp elongates and becomes narrower, the large mesial denticle persists and the lateral one enlarges, adding a small one nearer the base of the cusp. After the 16th tooth the cusps become simpler and smaller. The five outermost teeth are degenerate. This is a common type of radula in tropical Aplysias, but differs from most in the irregularity of the denticulations.

Caecum inflated at the apex, lying straight on the surface of the digestive gland, with its tip bent inwards.

Cerebral ganglia fused, visceral distinct.

SPECIFIC CHARACTERS

Aplysias of moderate size, purplish black in colour, with vertical bands of dark and light on the inner sides of the parapodial edges, and a triangular light patch anteriorly. Highly mobile and strongly contractile. Cephalic tentacles fimbriated, also the parapodia and anal siphon. Foot of moderate width with short tail. Penis long and filiform. Mantle thin with a small tubular aperture. Purple gland present. Opaline gland compound with a single conspicuous aperture. When preserved the animal may assume a short broad ballooned shape.

West Africa.

Subgenus **Aplysia** Linnaeus, 1767

Aplysia (Aplysia) cedrosensis Bartsch & Rehder, 1939 : 2

Text-figs. 39 and 40

Distribution. Lower California. Named by the authors from Cedros Island in the Gulf of California.

Material examined. The type, in the United States National Museum (No. 472859), and another specimen, which had been in the same Museum unnamed since 1889 and came from San Bartolomé Bay, Mexico.

This is one of the bulkiest members of the genus, and is so much enlarged posteriorly that it bears a superficial resemblance to a *Dolabella*. The type measures 165 mm. long, 90 mm. broad and 85 mm. high, but it must be much larger when alive. The general shape is low and very broad (Text-fig. 39*a*). The skin is tough and leathery, rough and caruncalate, black and brown all over, but described as grey originally, with black patches and an elongated black band dorsally posterior to the rhinophores. Mantle and inner sides of the parapodia mottled and blotched irregularly. The head is not much contracted, the neck thick, the parapodia short and exposing the whole of the dorsal area.

The broad head is clumsy, the cephalic tentacles widely separated, hardly rolled at the edges, not continued to the mouth. Eyes small on clear areas of skin. Rhinophores conical, stout, slit half-way down, wide apart.

Foot very broad, 118 × 70 mm. in the type specimen, rounded in front, with a tendency to form lateral wings, the edges defined, the tail short, broad, round, strongly contracted and bent ventralwards, so that it is difficult to determine whether it was sucker-like ; it is thick and tough. The penis and penis sheath exhibit clearly the characters of the subgenus (Text-fig. 39, *c*, *d*, *e*). The penis is black, very large and stout, being 54 mm. long and 11 mm. broad at the base, but tapering to a point. The sperm groove extends nearly to its tip. The penis sheath is divided as usual into two portions, a ridged muscular proximal part near the aperture and a basal distal part which in this species, although swollen, is not large enough to contain the whole of the penis, even when it is bent back on itself. The bulbous portion is lined with warts which in the type specimen are simple and strong, in the second specimen more slender and sometimes branched. Each wart bears simple spines, slightly recurved and probably of a horny or chitinous composition. The parapodia are small, short, widely separated anteriorly, giving a broad neck region. They are

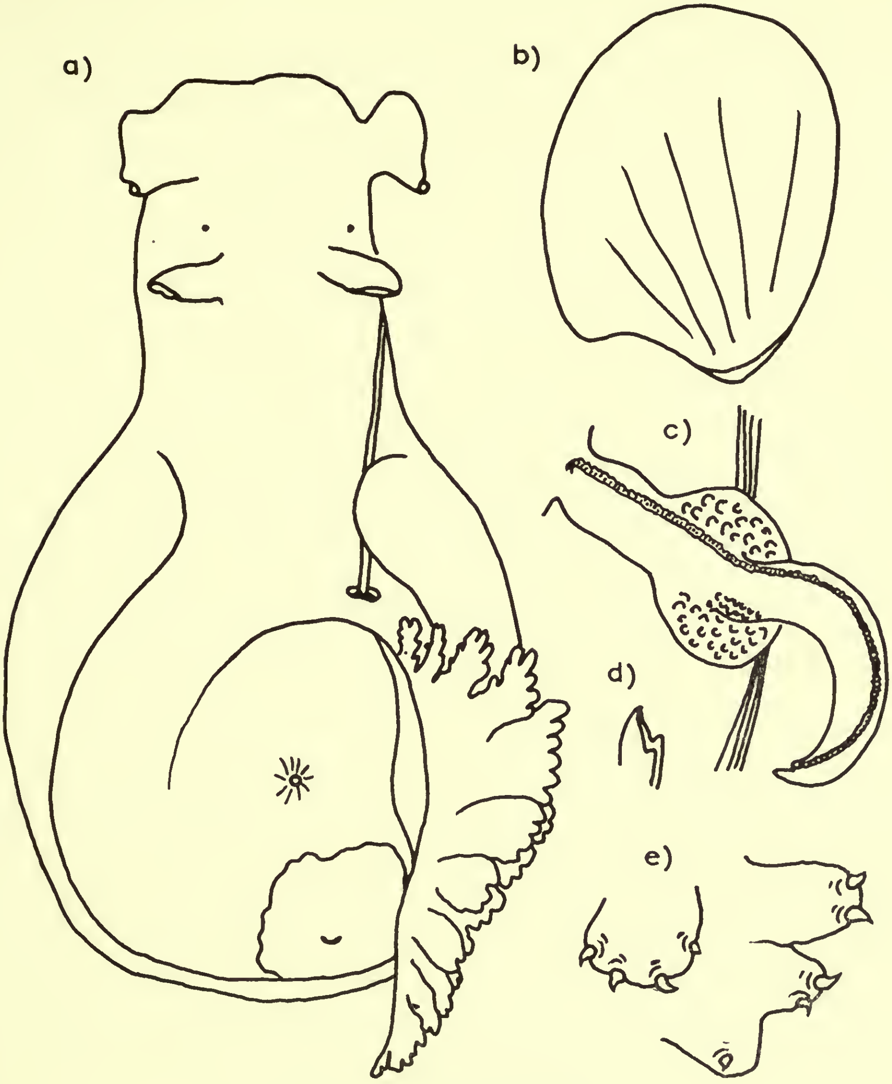

FIG. 39. *Aplysia cedrosensis.*

(*a*) The type specimen in dorsal view. Modified from the sketch by Bartsch & Rehder, 1939. The mantle is a little foreshortened and the mantle edge has been reflected. The ctenidium has been lifted out of the mantle cavity to show its size. × $\frac{2}{3}$.
(*b*) Shell in ventral view. × $\frac{2}{3}$.
(*c*) Penis sheath opened to show the bulbous warted region and the large penis. × $\frac{2}{3}$.
(*d*) Penis tip. × $1\frac{2}{3}$.
(*e*) Warts and spines from the distal portion of the penis sheath. × 21.

rather tight over the dorsal area and do not close it, and are very thick and rough. Posteriorly they unite to form a wall about 25 mm. high, shutting in the mantle cavity.

Mantle short and broad, not covering either the ctenidium or the genital aperture. There is a small, round, flat foramen with radiating lines of contraction around it. The anal siphon, 20 × 35 mm., is broad but not high, strongly attached to the mantle, flat on the side of it and only free for 5 mm.; it is therefore non-tubular (cf. *A. dura*, p. 362). The edge of the siphon is irregular but not fimbriated. Glands are present under the small mantle flap, but no information is available regarding the colour of their secretion.

Mantle cavity small, ctenidium large and projecting. Opaline gland of simple vesicles, multiporous. Genital aperture large and frilled, genital groove deep, with strongly developed dorsal lip.

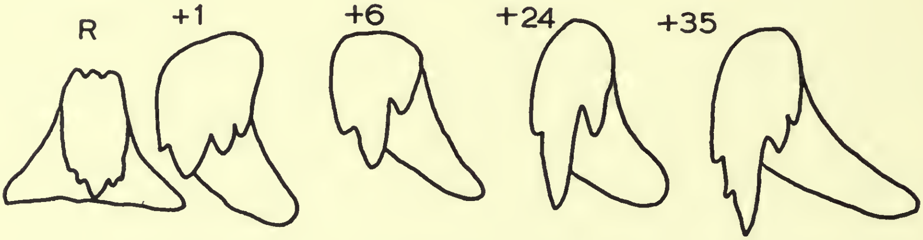

FIG. 40. *Aplysia cedrosensis.* Radular teeth. Rhachidian, first, sixth, 24th and 35th laterals. × 80.

Shell (Text-fig. 39*b*) large and broad, 76 × 57 mm., thin and flat, dark brown in colour. Growth lines are well marked and there are radiating ridges from the apex. No calcareous matter is present, but Bartsch & Rehder report slight calcification. No spire, but a slight turn-over at the apex. Anal sinus short and shallow, with the broad outer angle characteristic of the subgenus.

Radula (Text-fig. 40) very large, with 118 rows and a formula of 80.1.80. Rhachidian tooth pale and sunken, rather high, with narrow head and broadening plate. Cusp shorter than the plate, with a pair of denticles near the tip ; these get worn away in older teeth, as does also the cusp itself. First lateral with a broad head and short plate, short cusp with one denticle on each side, not forming a pair, the mesial denticle nearer the point than the lateral one. This applies also to the other teeth in the row, all of which are simple, although they have longer and more curved plates, narrower heads and longer and more acute cusps. Some of the outer laterals may develop two denticles mesially, but on the whole the radula resembles closely that of *A. juliana*. There are three vestigial teeth at the end of the row.

Cerebral ganglia forming a fused band, visceral ganglia joined.

SPECIFIC CHARACTERS

Large bulky shape, much enlarged posteriorly, skin thick, rough, leathery, dark in colour and mottled and blotched with brownish black, but without regular pattern.

Head broad, flat and clumsy, foot broad, parapodia small, low, thick, joined posteriorly to shut in the mantle cavity; mantle foramen round, flat; anal siphon non-tubular, wide, flat on the side of the mantle; shell broad, flat, without spire, but with short shallow anal sinus and large outer angle; radula large, simple, with many rows (more than 100) and numerous teeth in a row (up to 80). No information on the secretion of the mantle glands, but the inference would be that they secrete a milky substance, not purple.

Lower California.

Aplysia (Aplysia) depilans Gmelin, 1791 : 3103 (see pp. 274 and 396).

Text-fig. 41, *a–e*

The type species of the genus.

SYNONYMY : *Laplysia depilans* (= one kind of *Lernaea* of Bohadsch, 1761 : 49), and *L. d. major* Barbut, 1783 : 32.
Dolabella fragilis Lamarck, 1822 : 42.
Dolabella laevis de Blainville, 1819 : 395.
Aplisia leporina delle Chiaje, 1822 : 28.
A. poli delle Chiaje, 1822 : tav. 3.
A. poliana delle Chiaje, 1822 : 30.
Aplysia major Lankester, 1875 : 13.
A. melanopus Couch, 1870 : 173.
A. petersonii Gray, 1828 : 4, pl. 4 fig. 4 : Sowerby, 1869 : pl. 2.

DISTRIBUTION. Mediterranean, Atlantic coasts from France and the Channel Islands to West Africa (Morocco, Rio de Oro), Madeira. Rarely on the southern British coasts.

MATERIAL EXAMINED. Specimens from the Mediterranean and French Atlantic coasts.

The specific name is due to the erroneous belief that handling the living animal causes the hair to fall out. Rang (1828 : pls. 16 and 17) gave excellent figures of the animal. Mazzarelli's monograph on the Aplysiidae of the Gulf of Naples (1893) included an account of the three Mediterranean species, with coloured figures. In *depilans* (1891 : 3) he noted the spiral apex of the shell in the juvenile, the nodosities on the penis sheath and the spiral caecum. These nodosities had first been seen and recorded by Bohadsch (1761) and were figured by delle Chiaje (1828 : pl. 2).

Large Aplysias, low and broad, in contrast to the narrowness and height of *A. fasciata*, bulky, attaining 300 mm. in length when alive, 200 mm. long, 100 mm. wide and 80 mm. high when preserved. Skin smooth and firm. Colour variable, brown to greenish brown, dark, with large white or grey blotches, and fine dark veining. There may be a violet border to the tentacles, rhinophores, parapodia and the foot sole. Mantle speckled brown. Inner sides of the parapodia blotched with dark and light patches. All colour may disappear with preservation. The animal secretes abundant supplies of a milky white substance from the opaline gland, with a strong odour of musk. Extreme irritation, as noted by Mazzarelli (1889 : 582) and Engel (1957 : 241) may tinge this secretion with purple, but it is not clear whether the colour comes from one of the secreting glands or from the skin. The species is a clumsy swimmer.

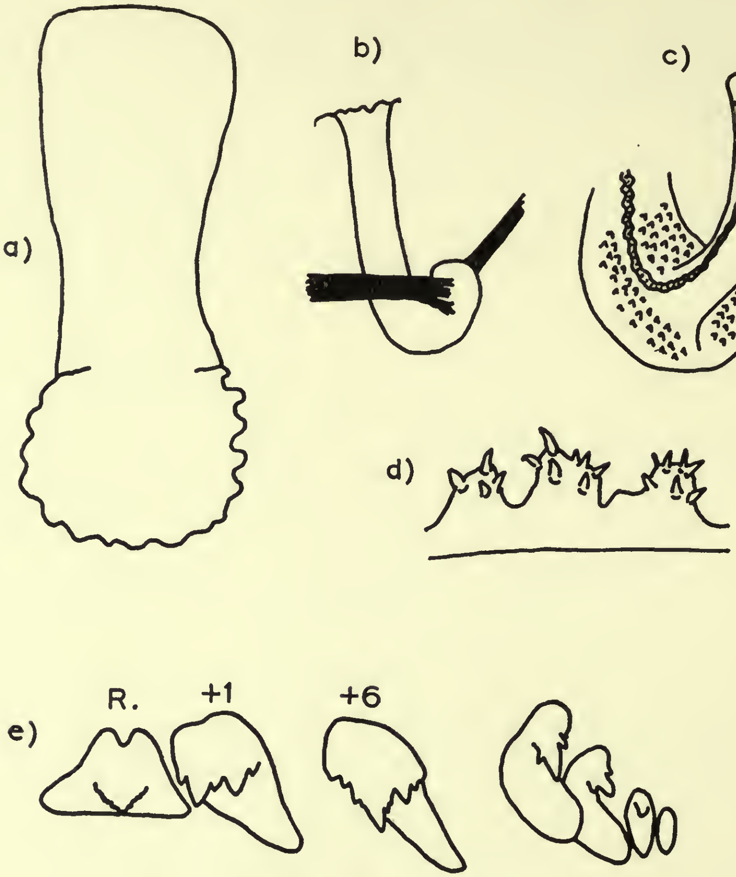

Fig. 41. *Aplysia depilans.*

(*a*) Foot sole to show sucker. × $\frac{2}{3}$.
(*b*) Penis sheath and retractor muscles. × $1\frac{1}{2}$.
(*c*) Penis sheath opened to show the penis and the nodosities on the lining of the distal portion of the sheath. × 2.
(*d*) Three of the warts, with their numerous small spines. × 16.
(*e*) Radular teeth. Rhachidian, first, sixth and outermost lateral teeth. Two of the last are turned on their sides to show the bulbous basal plates. × 80.

Head broad, neck short and thick, but both head and neck are narrower than the foot and the head projects forwards in front of the foot. Cephalic tentacles short and stout, rolled at the edges, linked by rounded lobes to the sides of the mouth. Eyes plain. Rhinophores widely spaced, conical, slit almost to the base.

Foot broad, 35 mm. wide in a specimen 120 mm. long, rounded and winged anteriorly, short and rounded posteriorly, in some specimens forming a distinct sucker (Text-fig. 41*a*) (cf. *juliana*, p. 365). Penis (Text-fig. 41*c*) broad, black, in a swollen recurved basal portion of the sheath (Text-fig. 41*b*), which is anchored by two stout retractor muscles and has a lining covered with wart-like swellings armed with spines (Text-fig. 41*d*). Parapodia widely spaced at their origins, close behind the rhinophores, rounded, smooth edged, not large, joined high up posteriorly, shutting in the mantle cavity.

Mantle with oval or round rayed aperture to the shell cavity, and short broad siphon. Mantle glands secrete a white substance.

Mantle cavity closed behind, ctenidium of moderate size, opaline gland large, reniform, pigmented, composed of simple vesicles each opening separately to the mantle cavity. Genital aperture pigmented, plain or with its edge curled in a spiral, hardly covered by the mantle, but well within the protection of the parapodia. Genital groove deep, with overhanging dorsal lip.

Shell 38 × 25 × 3 mm. in a 120 mm. specimen, narrowly ovate, beautifully shaped, firm, clear, with concentric and radiating ridges. Hardly any turn-over at the apex, but a recurved edge dorsally. Anal sinus wholly posterior, deep and short, with a large outer angle. A strong calcareous layer is present in the fresh condition.

Jaws small, crescentic or nearly rectangular, 9 × 3 mm. Rods of moderate length, straight and rounded at the tips.

Radula (Text-fig. 41*e*) large, up to 80 rows, formula 40.1.40. Rhachidian tooth pale, feeble, with short, high basal plate, straight posteriorly and only slightly incised anteriorly. Cusp very short and rounded, with a few indistinct irregular denticles. First lateral with an almost triangular plate, broad head, very short obtuse cusp and a few small irregular denticles, and one large lateral denticle. Remaining laterals with narrowed but still triangular plate, broad head, longer cusp with irregular denticles and larger ones both mesially and laterally. Two very small vestigial teeth at the end of the row. A simple type of radula.

Caecum large, its tip curled inwards like a crozier and only the stalk exposed on the surface of the digestive gland.

Cerebral ganglia small, fused. Visceral ganglia distinct, with large granular nerve cells.

Specific Characters

Large Aplysias, with low broad shape, smooth skin, dark brown or greenish brown colour with white or grey blotches and fine veining in black. Secrete a milk-white fluid with a strong odour of musk. Foot broad, with a rounded sucker posteriorly. Penis stout, black, the bulbous portion of its sheath armed internally with spiny warts. Parapodia joined high posteriorly, forming a wall round the mantle cavity. Opaline gland large, reniform, pigmented, simple, multiporous. Shell with broad anal angle and posterior anal sinus. Radula with many rows and numerous teeth in a row, simple, with few denticles. Caecum crozier-shaped.

East Atlantic from France to West Africa ; Mediterranean.

References (*see also synonyms*)

Blochmann, 1884 : 32.
Bohadsch, 1761 : 49, as *Lernaea.*
Bosc, 1802 : 63, as *Laplysia.*
delle Chiaje, 1828 : 28, 41, 72.
Grigg, 1949 : 795.
Mazzarelli, 1891 : 3 and 36.
Perrier and Fischer, 1908 : 1335.
Pilsbry, 1895 : 69, as *Tethys.*
Rang, 1828 : 64.
Vayssière, 1885 : 54, 65 ; 1935, No. 20 (not paginated).

Aplysia (Aplysia) dura sp. nov.

Text-figs. 42 and 43

DISTRIBUTION. Tristan da Cunha, South Atlantic Ocean, Cook Strait, New Zealand.

MATERIAL EXAMINED. Two specimens from the inshore waters of Tristan da Cunha, taken in the summer of 1952 by Mr. H. F. I. Elliott, and presented by him to the British Museum (Natural History). The larger specimen, chosen as the holotype, was given the number B.M. (N.H.), 1957.6.11.1.

A third specimen came from Lyall Bay, Cook Strait, New Zealand, and is now in Wellington Museum, New Zealand, after examination by me.

The type specimen measures 130 mm. long, 54 mm. wide and 54 mm. high ; it is thus of medium size, low and elongated (Text-fig. 42). Its proportions are unusual, for the broad head and long neck are followed by a small mantle and shell area and very small low parapodia. The head, including the cephalic tentacles, is 45 mm. wide, the rhinophores are 17 mm. apart and are placed mid-way between the cephalic tentacles and the commencement of the parapodia, which are 30 mm. apart at their origin. The mantle is 45 mm. long, 30 mm. wide, the foot 106 × 40 mm. Black pigment, partly bleached, is present on the tentacles, the outer sides of the parapodia, the genital aperture and groove, and a little is left on the ctenidium. The inner sides of the parapodia are blotched with black, the foot is intense black. There is no trace of colour other than the black pigment. Skin very tough and hard, but smooth, without a wrinkle.

Head broad, projecting well in front of the foot. Cephalic tentacles small, rolled on the edges. Eyes widely spaced on clear skin areas. Rhinophores wide apart, short, stout when contracted. Neck of the same width as the head.

Foot broad, tough, rounded in front, with a round sucker posteriorly, tail short, projecting behind the parapodial fusion. Penis (Text-fig. 43*b*) very large, stout, smooth, black. Bulbous portion of the penis sheath with two strong retractor muscles and lined with rounded, much branched wart-like swellings bearing spines. The warts (Text-fig. 43, *b*, *c*) are arranged in rows parallel with the sperm groove, the rows occurring in sets of from two to three rows, separated by smooth areas. On the side furthest from the sperm groove the warts are scattered and they are massed around the base of the penis itself. The warts are elaborately branched, with a number of spines on each branch. Parapodia small, thick, short and low, but possibly much contracted. They have little flexibility, and are joined posteriorly

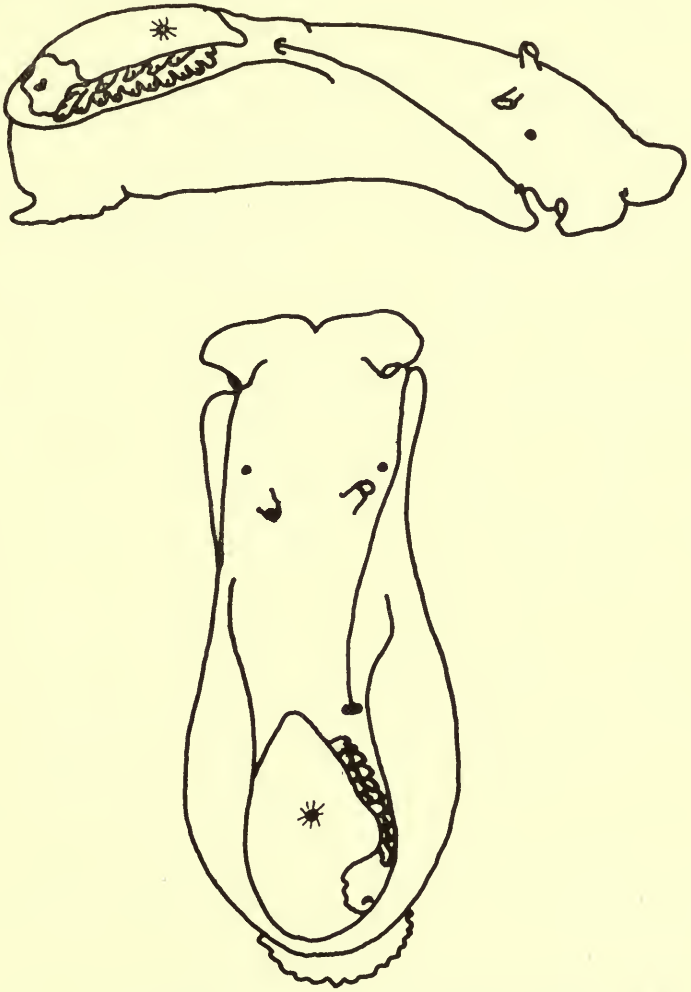

FIG. 42. *Aplysia dura*. Lateral and dorsal views. × $\frac{2}{3}$.

forming a mantle cavity pocket, but they do not cover the anal siphon, mantle or ctenidium.

Mantle very small, sharply pointed anteriorly, without overhang here. Mantle foramen small, flat, with black radiating lines. Anal siphon short, broad, flat, non-tubular.

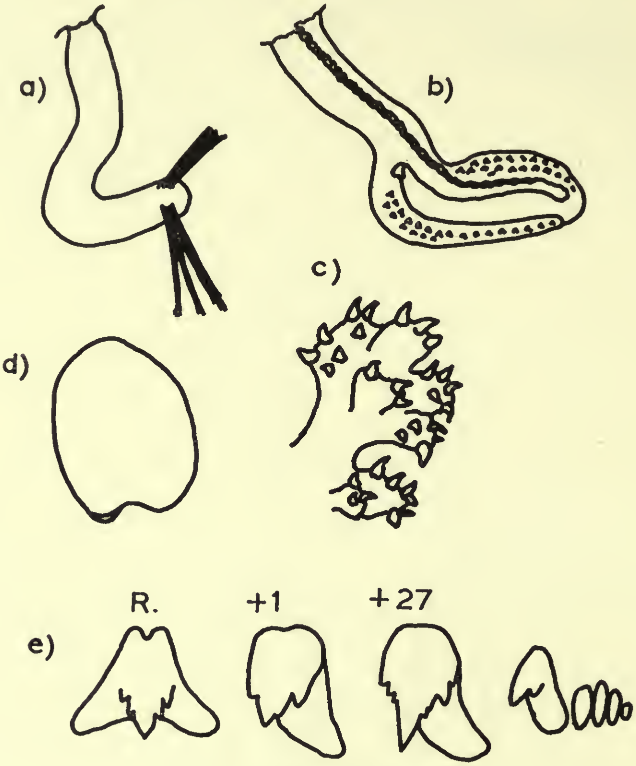

FIG. 43. *Aplysia dura.*

(*a*) Penis sheath and retractor muscles. × 1½.
(*b*) Penis sheath opened to show the seminal groove, penis and nodosities of the distal part of the sheath. × 2.
(*c*) A group of the branched nodosities with their numerous stout spines. × 16.
(*d*) Shell in dorsal view. × ⅔.
(*e*) Radular teeth. Rhachidian and first, 27th and outermost laterals. × 80.

Mantle cavity small, closed behind. Opaline gland small, simple, hidden beneath the muscles of the mantle cavity floor, multiporous. Genital aperture exposed (i.e. not covered by the mantle), large, inflated, spiral or smooth.

Shell (Text-fig. 43*d*) 40 × 26 mm., narrow and flat. Horny layer thin, with concentric lines ; calcareous layer dense, thrown into folds on the edges. No spire, anal sinus short and shallow, with the usual broad angle laterally.

Jaws long and narrow, 15 × 4·5 mm. Rods short, curved.

Radula (Text-fig. 43*e*) large and powerful, 20 × 13 mm., at least 90 rows and formula up to 50.1.50. The teeth are simple, but the denticulations are more pronounced than in *juliana*. The last four vestigial teeth are very small.

Salivary glands wide and flat. Caecum large, inflated at the apex, crozier-shaped.

Cerebral ganglia fused to form a flat band, even the pleuro-pedal mass fused.

SPECIFIC CHARACTERS

The species belongs to the subgenus *Aplysia*, as shown by the low, broad shape, broad foot, fused parapodia, broad siphon, simple opaline gland, spiny warts on the penis sheath, short broad pigmented penis, shape of the shell, simple denticulations of the radular teeth, broad salivary glands, crozier-shaped caecum. But the tough but smooth leathery skin, elongated shape, small mantle, shell and visceral regions, non-tubular anal siphon, weak opaline gland, more elaborate warts on the lining of the penis sheath, and more strongly denticulate, though still simple radula, are specific.

South Atlantic ; South Pacific.

The species resembles *A. cedrosensis* from Lower California in its shape, non-tubular siphon, small mantle and shell, but differs in the smoothness of its skin and in its relatively small visceral region.

Aplysia (Aplysia) juliana Quoy & Gaimard, 1832 : 309

Text-figs. 44, 45 and 46 *a*, *d*, *e*.

SYNONYMY : *badistes* Pilsbry, 1951 : 1.
[1]*bipes* Pease, 1860 : 23, as *Syphonota*.
capensis O'Donoghue, 1929 : 14, as *Tethys*.
juliana var. *quoyana* Engels & Eales, 1957 : 86, fig. 16*a*.
?*parva* Pruvot-Fol, 1953 : 38 (see p. 273).
petiti? Risbec, 1929 : 56.
rangiana d'Orbigny, 1837 : 210.
sandvichensis Sowerby, 1869 : pl. 4.
sibogae Bergh, 1905 : 4 ; Baba, 1937 : 211 ; 1949 : 24.
woodii Bergh, 1908 : 12.

Rang's *sorex* (1828 : 57) is a species dubia, as the specimen in the Paris National Museum does not agree with the description, and is probably not the type (see Engel & Eales, 1957) ; but specimens identified by various authors as *sorex* are usually juveniles of *juliana*.

DISTRIBUTION. World-wide in warm seas. Western Atlantic from Florida to Brazil, including the West Indies ; Eastern Atlantic : Morocco, Ghana and the Canary Islands ; Indian Ocean : the Seychelles, Mauritius, Madagascar, Kenya to the Cape, India and Pakistan ; in the Western Pacific : Japan, China, Formosa, the East Indies, Polynesia, Australia, Tasmania and New Zealand ; Eastern Pacific :

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[1] The only species of Pease which can be identified with certainty.

California, Galapagos and Peru. There is one record from the Mediterranean, the Naturhistorisches Museum of Vienna having three specimens from the harbour of Algiers.

MATERIAL EXAMINED. Numerous specimens from all parts of the world.

A. juliana is the most variable species in the genus, and appears to be undergoing marked changes in size, form and colour, without anatomical distinctions large enough to warrant separation into different species at present. Because of its wide range, round the whole world in tropical and sub-tropical seas, one would expect to find variations, but it is remarkable that more than one variation occurs in the same area. The species was founded by Quoy & Gaimard (1832) from specimens taken in the Indian Ocean and figured by them.

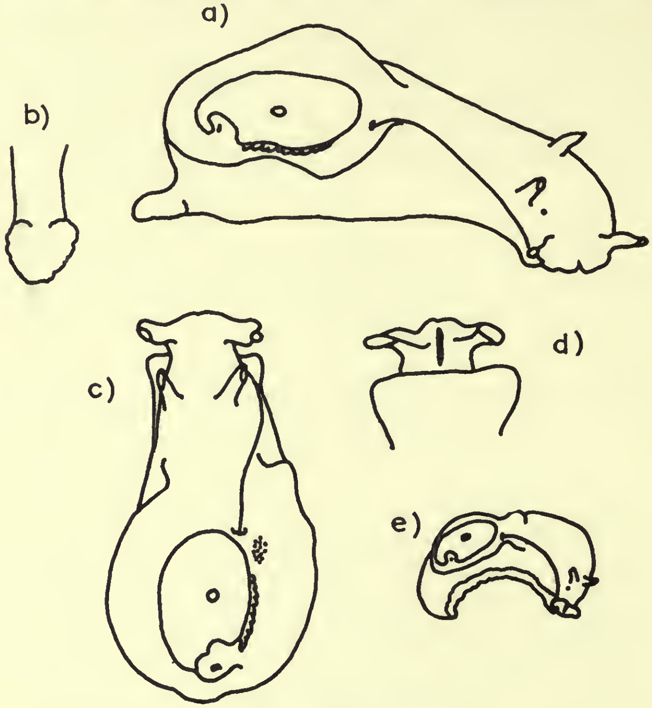

FIG. 44. *Aplysia juliana.*

(*a*) Lateral view of a specimen from Tasmania, var. *bipes*. × 1½.
(*b*) Posterior end of the foot to show the sucker. × 1½.
(*c*) Dorsal view of a specimen from New South Wales. × ⅔.
(*d*) Head of this specimen in ventral view. × 1.
(*e*) Lateral view of a young specimen from Grand Canary to show partial "curling up in a ball" and the characteristic pinching in of the parapodia anterior to the mantle. × ⅔.

Medium to large, bulky Aplysias, the largest reaching 300 mm. when alive and more than half this when preserved (Text-fig. 44, *a*–*e*). The general shape is low and broad with the visceral hump set far back. Colour very variable—yellowish green, reddish yellow, dark green, olive, brown, ash grey, or sooty black. There may be markings on the sides of the body and the inner sides of the parapodia, mantle and mantle cavity floor, tentacles and foot. The edges of the foot may be violet in colour. There are usually fine black reticulations or the markings may be darker than the ground colour and quite irregular, sometimes in the form of ragged brown or black spots, with large and small white flecks and stripes. The skin is smooth, but may roughen on contraction or form patterns similar to those seen on leather. The contracted animal may assume the sitting hare position and draw in the head considerably, or it may curl up in a ball, a condition more commonly seen in juveniles. Macnae, in a personal communication, notes the peculiar mode of progression of the living animal, which may glide along the surface, or loop along like a caterpillar, fastening itself to the substratum by adhesion of the anterior and posterior portions of the foot, where the chief pedal glands are situated. In fact the posterior pedal glands are especially well developed, as in other members of the subgenus, and the foot contracts in this region to form a rounded or heart-shaped sucker. Upon this character Mme. Pruvot-Fol founded the subgenus *Tullia*, but did not realize that it is also true of *A. depilans*, the type of the genus. The sucker, however, is evident only when the glands are in a state of secretion, and in a given batch of specimens, some will show it well, others feebly and some not at all. The animal has a strong smell of musk and when handled exudes copious quantities of an opalescent white fluid from the opaline gland on the floor of the mantle cavity. Macnae kindly checked this for me on South African specimens. There is no purple secretion from the mantle glands.

G. P. Whitley of the Australian Museum, Sydney, in notes dated June 1924, described the egg strings as light to dark yellow, and measured a string of 865½ inches, or more than 72 feet.

Head broad, low and clumsy, with a long but strongly contractile neck. Cephalic tentacles flattened, rolled at the edges, quite separate dorsally but joined ventrally to each side of the mouth slit. Eyes larger than usual, but may be hidden in contracted animals. Rhinophores stout, rather small, round when contracted, wide apart.

Foot broad, with rounded edges anteriorly; in a well expanded specimen there may be lateral wings. Posteriorly there is the sucker above mentioned. The penis sheath (Text-fig. 45*a*) is large, heavily pigmented, and divided into two portions, of which the lower or distal part is bent back on the proximal part, and is attached laterally by two strong retractor muscles. The proximal part is muscular, ridged internally, with a marked continuation of the spermatic groove. The distal or bulbous part is thinner and is lined by numerous simple and compound ingrowths or warts, each bearing on its summit small curved spines, which appear to be of a chitinous nature (Text-fig. 45*b*). Young specimens have the warts but no spines. The arrangement of the warts varies; in some specimens they are scattered, in the variety *bipes* they are in rows and groups of rows. They may also spread along the penis itself, around its base or along the side not occupied by the spermatic groove. A specimen from Formosa had a single row of warts reaching almost to the tip of the penis. The penis (Text-fig. 45*c*) is short, dark, very broad and conical; the spermatic groove runs straight along it to near the spoon-shaped tip. Parapodia large, evenly rounded, thick and fleshy, freely mobile, natatory, joined posteriorly high up, forming a deep posterior mantle cavity pocket. Normally the dorsal area is widely exposed, but the parapodia can close over the mantle region.

Mantle large, thin, about half the length of the contracted animal. Overhang wide, covering the large ctenidium. Shell foramen oval, smooth walled, flat, contractile, sometimes ringed with pigment, rarely rayed. Anal siphon short, wide and thin, tubular and sometimes fluted along the edges. Mantle glands present, but the fluid secreted is white, not purple.

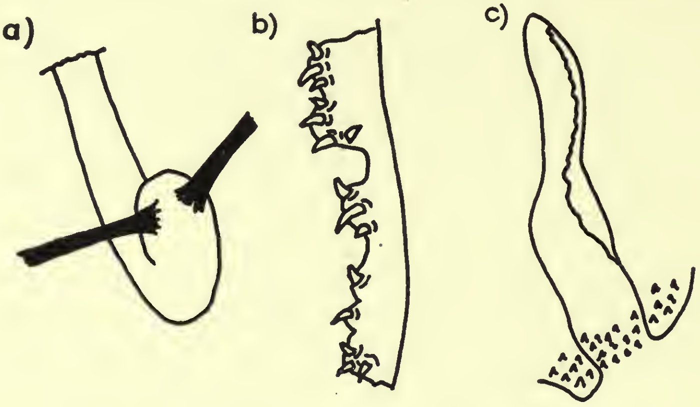

FIG. 45. *Aplysia juliana*. Penis and penis sheath.

(*a*) Penis sheath with its retractor muscles, from a New Zealand specimen. × 1½.
(*b*) Portion of the wall of the distal portion of the sheath of the same specimen. × 16.
(*c*) Penis of an Australian specimen, with spiny warts clustered round its base. × 2½.

Mantle cavity extensive, with a large pigmented ctenidium and kidney shaped, grey, simple, multiporous opaline gland. Genital aperture smooth and crescentic, usually large, strongly pigmented and becoming inflated in the sexually mature animal. It is exposed, i.e. not covered by the mantle. The genital groove is strongly marked.

Shell (Text-fig. 46, *a*, *d*) variable according to age and habitat, large for the size of the animal, but either broad or narrow. In a specimen from Kurachee (= Karachi) the length was 1·2 times the breadth; in a New Zealand specimen the length was 1·5 times the breadth, giving broad and narrow shells respectively. In general, Pacific specimens tend to be narrower than those from the Indian Ocean. One character, however, is more constant. The angle made by the anal sinus and the right border of the shell, usually referred to as the anal angle, is almost a right angle. The shell is not very concave, has a shallow anal sinus, an incurved apex without spire and both horny and calcareous layers. Very young specimens may exhibit a spiral apex (Marcus, 1955 : fig. 29).

The jaws are large curved plates of straight or slightly curved, elongate rods.

Buccal mass large, radula characteristic (Text-fig. 46*e*). The number of rows of teeth is high and may reach more than 70, and the formula 40.1.40. The feature of the dentition is the simplicity of the serrations on the teeth. Rhachidian tooth pale and feeble, with a moderately broad basal plate, narrower and deeply excavated anteriorly. The cusp is shorter than the plate and has a few irregular small denticles,

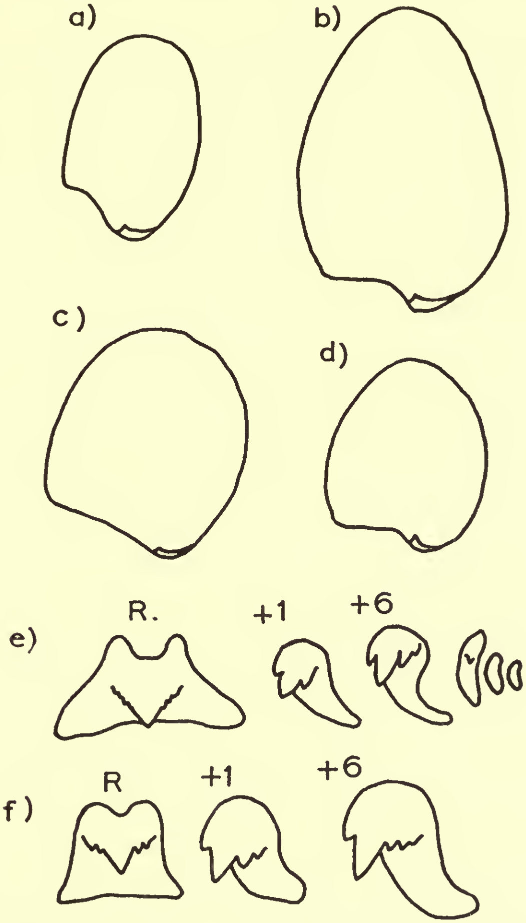

FIG. 46. *Aplysia juliana* (*a*), (*d*), (*e*). *Aplysia nigra* (*b*), (*c*) (*f*). (*a–d*) shells in ventral view, × $\frac{2}{3}$; (*e–f*) radular teeth, × 80.

(*a*) Shell of *A. juliana,* Australian specimen var. *bipes* (narrow type).
(*b*) Shell of *A. nigra* (narrow type), New Zealand specimen.
(*c*) Shell of *A. nigra* (broad type), Australian specimen.
(*d*) Shell of *A. juliana,* specimen from Kurachee, Pakistan (broad type).
(*e*) *A. juliana,* Australian specimen, var. *bipes.* Rhachidian, first, sixth and outermost lateral teeth of the radula.
(*f*) *A. nigra* var. *delli* (New Zealand), rhachidian and first and sixth lateral teeth of the radula.

which disappear in older teeth. Laterals dark brown in colour, with short, outwardly-turned basal plates and short broad heads, the cusp short and plain, except in very young teeth, where it bears fine denticles and a single larger denticle on each side. The three outermost teeth are degenerate.

Salivary glands broad and flat. Caecum unusually long and curved inwards like a crozier, or spirally coiled near the tip (Text-fig. 8*d*).

Cerebral ganglia contiguous within a connective tissue sheath, visceral ganglia more or less distinct.

The following varieties can be distinguished :

(*a*) The typical *juliana* is large, bulky and of a grey self colour with or without ragged spots. It inhabits muddy estuaries in the inshore period and occurs in all areas.

(*b*) The var. *bipes* is narrower and smaller, and occurs on the islands in the Pacific, on the coasts of East Africa and the East Indies. The spiny warts on the lining of the distal part of the penis sheath are arranged in more regular rows than in the typical form.

Using the shell characters alone, two varieties can be distinguished :

(*c*) var. *quoyana*, with narrow shell (Text-fig. 46*a*).

(*d*) var. *sibogae*, with broad shell (Text-fig. 46*d*).

The last two varieties, however, overlap with those given above. Thus *bipes* is narrow shelled, and the typical *juliana* may be either broad or narrow shelled, according to locality.

Specimens from Australia carried the Copepod *Strongylopleura pruvoti* Monod & Dollfuss, 1932 on the ctenidium. This is the only species believed to be parasitic that is known to occur upon or within any member of the genus. It has also been found on the Australian species *A. sydneyensis* (see p. 350). Specimens were identified by Dr. J. P. Harding and have been deposited in the collections of the British Museum (Natural History).

Specific Characters

Colour and size variable, sooty black, or lighter, with ragged dark spots. Low, bulky body, broad foot with posterior sucker on the tail, used for adhesion during looping movements ; thick natatory parapodia joined high up posteriorly ; flat oval mantle foramen ; white mantle gland secretion ; white musky secretion of the simple, multiporous opaline gland ; large radula with feeble denticulations ; broad flat salivary glands and crozier-shaped caecum. The bulbous portion of the penis sheath lined with fleshy warts, each bearing several hard spines ; the penis pigmented, stout, with straight sperm groove. Shell variable, either broad or narrow, but with a near right angle between the anal sinus and the right border.

Circumglobal, approximately from 42°N. lat. to 46°S. lat.

References (*see also synonyms*)

Adams, H. and Adams, A., 1858, **2** : 33 as *julienna*.
Baba, Hamatani & Hisai, 1956 : 216, as *sibogae* (breeding habits).
Eales, 1957 : 179.

Edmonson, 1933 : 152, as *Tethys bipes*.
Engel & Eales, 1957 : 83.
Macnae, 1955 : 237.
Marcus, 1955 : 15.
Martens, 1880 : 307.
Ostergaard, 1950 : 99, as *bipes*, spawning.
Pilsbry, 1895 : 91, as *bipes* ; 108, as *juliana* ; 86, as *rangiana*, all as *Tethys*.
Pruvot-Fol, 1933 : 400 ; 1934 : 41 ; 1953 : 33, as *sorex*.

Aplysia* (*Aplysia*) *nigra d'Orbigny, 1837 : 209

Text-fig, 46 *b*, *c*, *f*.

SYNONYMY : *brunnea* Hutton, 1875 : 279.
hamiltoni Kirk, 1882 : 282.
hyalina Sowerby, 1869 : pl. 5.

DISTRIBUTION. Australia (New South Wales), New Zealand (North and South Islands), Brazil, Peru.

MATERIAL EXAMINED. Specimens from Australia and New Zealand. Dr. Marcus sent valuable information relating to living specimens collected on the Brazilian coasts. D'Orbigny gave an excellent figure of the animal, copied by Pilsbry.

This species comes very close to *A. juliana*, but the differences in size, colour, shape and certain anatomical characters indicate that, unless information to the contrary becomes available, it is advisable to retain d'Orbigny's specific name. The mollusc is large and bulky, reaching a length of 250 mm. The body is elevated and broad, the visceral hump being typically higher and more centrally placed than in *juliana*. The skin is tough and wrinkled when contracted, heavily and uniformly pigmented in black, brownish black or rich brown, usually without pattern, occasionally with clear areas appearing as white spots. The head, tentacles, sides of the body, foot, part of the mantle roof and mantle cavity floor, inner edges of the parapodia and the ctenidium are of an intense black or brown colour, but the pigment may fade with preservation and become grey or sooty.

Head broad, neck short compared with *juliana*. Cephalic tentacles broad, folded, continued to the ventral side of the mouth slit. Rhinophores thick, strongly contractile, slits short. Eyes small. Genital groove an intense black. Penis broad and spatulate, the enlarged bulbous portion of the sheath with both simple and elaborately compound (branched) warts bearing numerous spines. The warts are partly scattered and partly in regular rows.

Foot broad, front edges rounded, tail broad, rounded, forming a sucker. Parapodia thick, upstanding, commencing close behind but lateral to the rhinophores, capable of closing over the dorsal slit, united high up posteriorly, forming a deep mantle cavity pocket.

Mantle large, with considerable overhang and a small, oval or round aperture, contractile, sometimes with radiating lines. Anal siphon short and broad. Mantle glands colourless; d'Orbigny stated that it exuded a slightly violet and milky white secretion, Marcus (1956 : 43) described a black exudate, the local name of the animal being " tinteiro " or ink-well.

Mantle cavity extensive and deep, containing the large, thick, black ctenidium. The opaline gland varies from small to large and is involved in the muscles and fibres of the body wall; as usual in the subgenus it is multiporous and consists of simple gland cells. D'Orbigny referred to the strong odour of musk from the opaline gland. The genital aperture is inflated in the mature animal and becomes thick and fimbriated.

Shell large, broad and flat, measuring 44 × 37 mm. in a specimen 100 mm. long. Anal sinus wide but shallow, apex oblique, dorsal edge recurved posteriorly, anal angle almost a right angle but more rounded than in *juliana*.

Jaws composed of very tightly packed, curved, parallel-sided rods, some truncated and others pointed at the tips.

Radula large, with numerous rows and many teeth in a row. One specimen measuring 131 mm. when preserved had a radular formula of 100 × 60.1.60, a figure higher than that of any *A. juliana* examined, and with the teeth simpler, but with longer cusps to the laterals. The rhachidian tooth is feeble, in some specimens with hardly a central cusp, and without denticles such as the young tooth of *juliana* has. Laterals also without trace of denticles except for the single one on each side of the rather long, spiky cusp, which at about the middle of a row attains 1½ times the length of the plate. The outermost four teeth are degenerate, three of them especially so.

Cerebral ganglia fused, visceral ganglia large, separate.

The following varieties can be distinguished:

(*a*) var. *brunnea* resembles *nigra*, but is deep brown or brownish black all over. It has been recorded from New Zealand and Brazil.

(*b*) var. *delli* nov. Specimens from North Island, New Zealand, sent by Dr. R. K. Dell of Wellington, had an extension of the parapodial lobes downwards to the foot anteriorly, a lower fusion of the parapodia posteriorly, a papillate mantle aperture, a tall and leaf-like anal siphon and spiral genital aperture.

Specific Characters

Large size, heavy pigmentation in brown or black, usually without pattern but occasionally with clear areas on the sides of the body. Mantle aperture small, contractile, sometimes rayed. Mantle glands exuding white and black secretion; opaline gland a milky, odoriferous, mucous substance. Shell broad, rounded. Radula very large, with a high formula reaching 100 × 60.1.60, the teeth simpler than in *A. juliana* but with longer and more spike-like cusps to the laterals at the middle of the rows.

Australia, New Zealand, Brazil, Peru.

References (*see also synonyms*)

Allan, 1932*a* : 423 ; 1950 : 213, as *hyalina*.
Marcus, 1956 : 43, as *juliana*.
Pilsbry, 1895 : 85, as *Tethys nigra* ; 97, as *T. brunnea* ; 99, as *T. hamiltoni*.
Suter, 1913 : 545 and 1915 : pl. 23, as *brunnea*.

Aplysia (Aplysia) vaccaria Winkler, 1955 : 5, pls. 2, 3

Text-figs. 47–49

The holotype is in the Allan Hancock Foundation, University of Southern California, No. 983.

Distribution. Point Fermin, San Pedro, Palos Verdes and San Juan Capistrano, Southern California.

Material examined. A specimen from Doheny Beach State Park, San Juan Capistrano, California, sent by Dr. Winkler, and the gut, penis sheath and penis of another specimen from the same area also presented by him.

This large and bulky species was described from living specimens by Winkler (1955 : 5), who kept them alive in an aquarium, where they grazed cow-like on the seaweed *Egregia* (Text-fig. 47*d*). Alive they attained a length of 255 mm., a width of 135 mm. and a height of 110 mm., with a foot 100 mm. wide. Preserved, the specimen now in the British Museum (Natural History) measures 142 mm. long, 88 mm. wide and 65 mm. high, the foot being 110 mm. long and 62 mm. wide. The rhinophores of the living specimen were 40 mm. posterior to the cephalic tentacles and 20 mm. high. The parapodia were 60 mm. apart in front, and formed a wall 50 mm. high around the mantle cavity posteriorly. The body is stout, firm and smooth, of a deep purplish black colour, sometimes without markings, or with fine grey to white spots on the sides, head and parapodia. The foot sole is deep blue black. There is no odour. The species spawns in February and March, under rocks in shallow water, and is usually nocturnal in habit.

Head large, neck broad. Cephalic tentacles broad, folded, black, fimbriated. Rhinophores slender.

Foot broad, tough, with a short pointed tail and no trace of a sucker. Penis sheath (Text-fig. 48*a*) very large, bent back on itself, fastened by two stout retractor muscles attached to the bulbous portion, the black interior of which is lined for about half its width by branched swellings capped by curved spines, usually from three to five spines on each branch. A few small warts lie on the penis base (Text-fig. 48, *b*, *c*). Sperm groove white. Penis large, 18 mm. broad at the base, tapering to a fine point and curved. Genital groove running straight along the convex side of the curve nearly to the tip. Parapodia well developed, widely spaced in front, united behind high up, shutting in the mantle cavity. Some mottling on the inner sides but no definite pattern.

Mantle firm, with an aperture 10 mm. wide. Anal siphon tubular, crested, broad. Mantle glands secrete a sparse white secretion.

Mantle cavity closed behind, ctenidium striped black and white, opaline gland simple, with many apertures.

Shell (Text-fig. 47*a*) large, broad, 70 × 60 × 25 mm. in the holotype, rounded, rather thick, with both horny and calcareous layers, no spire but thickened edges fanning out from the apex. Anal sinus very shallow and short, the anal angle rounded but nearly rectangular. In the B.M. (N.H.) specimen the shell (Text-fig. 47, *b*, *c*) measures 60 mm. long and 43 mm. wide ; it is shallower, but is of the typical *Aplysia* shape.

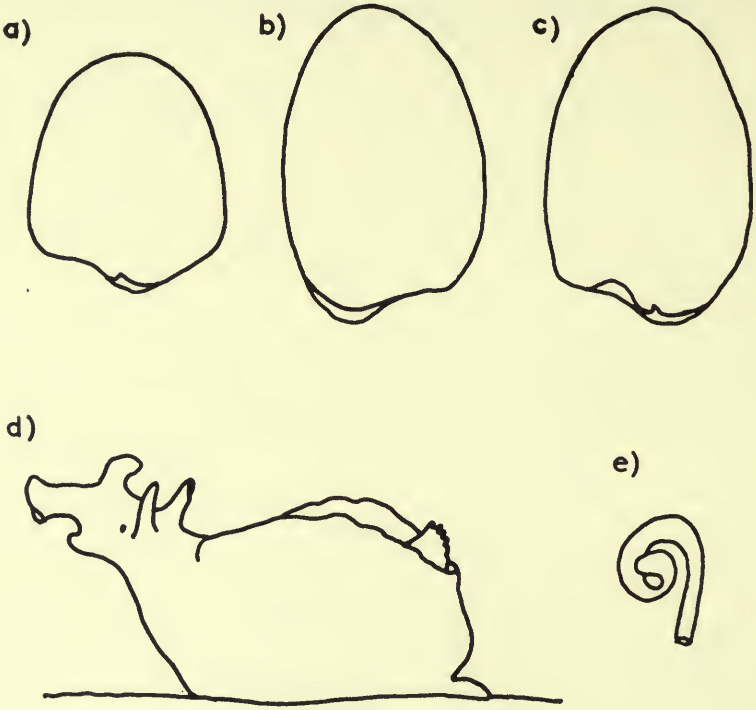

FIG. 47. *Aplysia vaccaria.*

(*a*) Shell in ventral view. After Winkler. × ½.
(*b*) Shell of B.M. (N.H.) specimen in dorsal view. × ⅔.
(*c*) The same shell in ventral view. × ⅔. In addition to the inturned apex, there is a thickening of the chitinous portion along the rim of the shallow anal sinus.
(*d*) The mollusc resting on the floor of an aquarium, raising the head as when browsing. After Winkler. × 2/9.
(*e*) Caecum. × 1½.

Jaws broad and rectangular, the rods tightly packed, short, straight, truncate or rounded at the tips.

Radula large, with at least 100 rows of teeth and a formula reaching 80.1.80, but may be less than this (Text-fig. 49). Rhachidian tooth pale, sunken, feeble, with narrow head and simple cusp hardly as long as the basal plate. First lateral with tapering, curved basal plate, rounded head and short cusp, bearing a short stout denticle on each side. The basal plates broaden and may become squared off further along the row, but are never very large. The heads are at first broad and rounded, then narrow. The cusps elongate considerably and become narrower, reaching their greatest length at about the middle of the row. They are longer than in any other species of the subgenus. Their denticles are weak throughout. About three teeth at the end of the row are pale, feeble and cuspless.

Salivary glands very broad and flat. Caecum long, the tip curved inwards in a spiral (Text-fig. 47*e*).

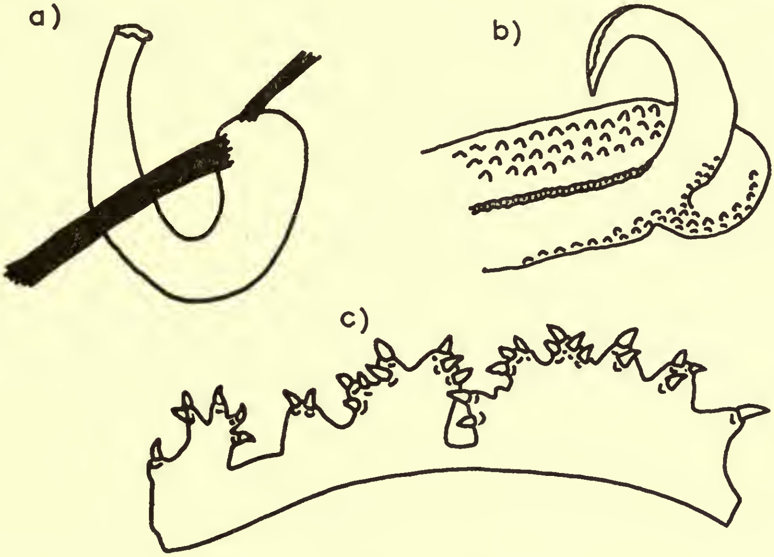

Fig. 48. *Aplysia vaccaria.*

(*a*) Penis sheath and retractor muscles. × $\frac{2}{3}$.

(*b*) Penis sheath opened to show, conventionally, the warted lining of its basal portion and the large, stout, pointed penis. A few warts extend along the convex side of the penis. The sperm groove is indicated by a double line; it runs up the convex side of the penis to near its tip. × $\frac{2}{3}$.

(*c*) A portion of the sheath wall to show the branched warts and spines. × 10.

The nerve ganglia exhibit complete fusion of the pairs, even the buccal ganglia are fused.

Specific Characters

Large, bulky Aplysias, with smooth skin, black coloration, broad dark foot with pointed tail on which no sucker has been observed. Penis large, black, in a bulbous sheath lined by branched spiny warts. Parapodia ample, joined high up behind. Mantle aperture large, flat, mantle glands secrete a white substance. Anal siphon tubular. Opaline gland simple, multiporous. Shell broad, thick, with shallow anal sinus. Radula large, with numerous rows and teeth in a row, all the teeth simple, but with cusps of considerable length. Caecum long, with spirally coiled apex.

Pairs of ganglia fused. The characters are those of subgen. *Aplysia*, except for the absence of a sucker on the foot.

Southern California.

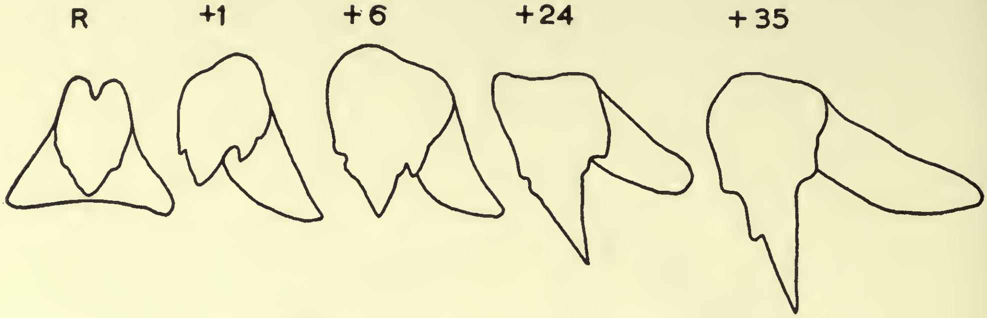

FIG. 49. *Aplysia vaccaria*. Radular teeth. Rhachidian and first, sixth, 24th and 35th laterals. × 100.

The species has affinities with *A. cedrosensis*, but the latter has a thick, warted skin, brown mottled coloration, flat, non-tubular anal siphon, simple warts on the penis sheath lining, and shorter cusps to the lateral teeth of the radula.

Subgenus **Phycophila** A. Adams, 1861

Aplysia (Phycophila) euchlora (Adams in M. E. Gray, 1850)

Text-fig. 50

SYNONYMY: *Placobranchus euchlorus* Adams in M. E. Gray, 1850, **2** : tab. 179 fig. 1, from a drawing by A. Adams ; **4** : 35 (Explanation of plates).
" *Aclesia euclorus* (*Pacobranchus e.*), Adams "[1] M. E. Gray op. cit. **4** : 98.
Aplysia (*Phycophila*) *euchlora* A. Adams, 1861 : 41.
Aplysia immunda Bergh, 1902 : 163 (juvenile).

DISTRIBUTION. Western Pacific : Japan (Adams's specimen) and Siam (Bergh's specimen and one in the B.M. (N.H.)).

MATERIAL EXAMINED. A single specimen from Siam (Text-fig. 50, *a–e*), labelled *A. mouhoti* Gilchrist, 1895, M. Mouhot's collection, numbered B.M. (N.H.), 1860.1.18.3. This specimen is not *A. mouhoti*, which is a synonym of *Syphonota geographica*.

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[1] The mis-spellings are in this section only of Mrs. Gray's work. The type-species of *Placobranchus* Hasselt is a nudibranch.

A. Adams gave a figure and a very imperfect account of his species. It was green, smooth, compressed, with narrow sole, elongated anterior tentacles, narrow rhinophores truncate at their apices, and long slender tail. Shell membranous, oblong, dilated in front, the apex not involute. It was found in the Strait of Tsugaru, Japan, crawling on floating weed. Bergh's specimen was a juvenile 17 mm. long, 9 mm. wide and 8 mm. high, elongated, on floating algae, from Siam. He described a network on the sides, with scanty black spots, and a median black band dorsally. Sole of the foot narrow, only 5 mm. wide. Inner sides of parapodia with strong black perpendicular bands joined at intervals. Mantle glands carmine. Radula 34 × 15.1.15.

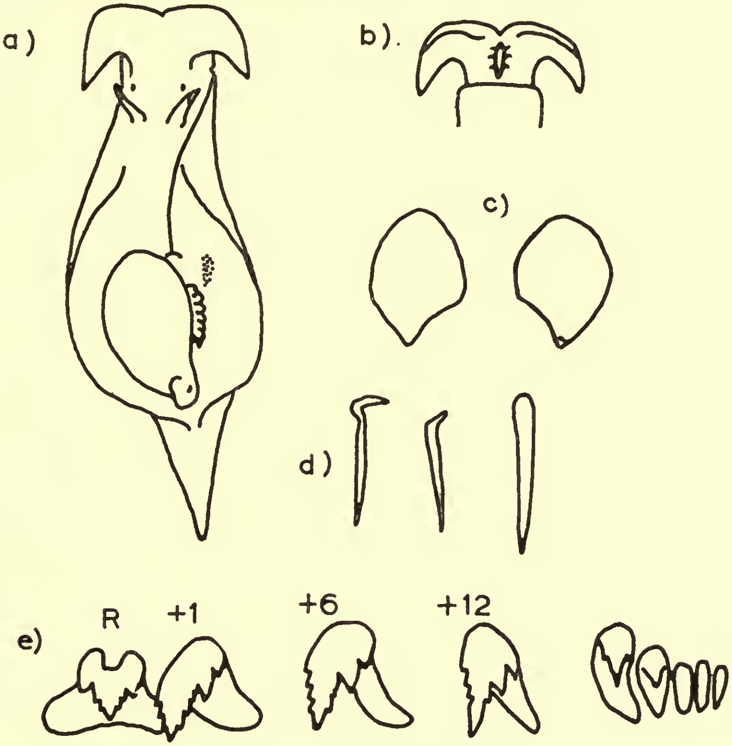

FIG. 50. *Aplysia euchlora.*

(*a*) Dorsal view. × 1.
(*b*) Head in ventral view. × 1.
(*c*) Shell in dorsal and ventral views. × $\frac{2}{3}$.
(*d*) Jaw rods.
(*e*) Radular teeth, Rhachidian, first, sixth, 12th and outermost laterals. × 80.

This meagre information on the species is hardly sufficient for identification, were it not for certain peculiar features. These are the extreme narrowness of the body and especially of the foot, the unusually long slender tail, and the posterior narrowing of the parapodia in Adams's figure. The British Museum specimen agrees so well with these features, and in its locality, Siam, that it must either be identified as *euchlora* or made into a new species. The following account is based on the assumption that it belongs to Adams's species.

The specimen (Text-fig. 50*a*) measures 65 mm. long, 20 mm. wide and 24 mm. high. It is soft and flabby, but not much contracted. There are remnants of black pigment on the sides and foot, but no definite markings. There are a few black marks on the inner sides of the parapodia, a little pigment on the ctenidium and the cephalic tentacles, but the rhinophores are colourless.

Head and neck narrow, the latter short. Cephalic tentacles (Text-fig. 50*b*) broad, hardly rolled on the edges but turned over along the anterior border, where they extend across the head anterior to the mouth, with a small central depression; laterally they are pointed and slope backwards. The rhinophores are short, close together, diverging, slender. Eyes rather large, anteriorly placed relative to the rhinophores.

Foot narrow, only 7 mm. wide, very soft and wrinkled, with round anterior border and long, pointed tail. Penis sheath small, not very muscular, its distal end recurved, with two small retractor muscles. Penis filiform, very long and narrow. Parapodia moderate, very thin on the edges, open widely exposing the mantle region, free and flexible, coming close together posteriorly over the foot, but hardly joined.

Mantle small, 18 × 15 mm., thin, delicate, without visible foramen or colour in the mantle gland. Anal siphon small, thin, projecting backwards in the specimen.

Mantle cavity exposed, ctenidium small, opaline gland reniform, simple, with many apertures. Genital aperture in front of the mantle, small, crescentic, genital groove feeble.

Shell (Text-fig. 50*c*) 26 × 18 mm., very delicate, oval, rather flat, with very small apex, anal sinus long, shallow. Remains of calcareous layer present.

Jaws small, very dark brown. Rods of exceptional length, closely and neatly packed, giving a tesselated appearance, some spatulate, others near the edge curved at the tips like birds' heads (Text-fig. 50*d*).

Radula (Text-fig. 50*e*) of dense brown colour but broken up. Buccal mass small. At least 40 rows and a formula 25.1.25. Rhachidian tooth with broad base, slightly curved behind and excavated in front, cusp at first longer than the basal plate, but shortening with wear, denticulations of the usual type in the genus. Laterals with short curved basal plates, tapering but becoming bulbous near the end of the row, with long, denticulate cusps. The last three or four teeth vestigial but unusually dark in colour.

Cerebral ganglia fused into a flat band, visceral ganglia joined.

SPECIFIC CHARACTERS

Small size, slender shape, very narrow foot and long pointed tail. Cephalic tentacles broad and of unusual shape, rhinophores slender, close together, eyes more anteriorly placed than usual. Penis filiform. Parapodia free, meeting on the tail. Mantle small, shell sac closed. Opaline gland simple, multiporous, genital aperture not covered by the mantle. Shell oval, flat, delicate, with long, shallow anal sinus.

Radula without special characteristics, but small and dark in colour. Cerebral ganglia fused. Habitat on floating weed.

North Pacific Asiatic area.

3. GEOGRAPHICAL DISTRIBUTION

Distribution of the species of *Aplysia* is limited by three factors—the life history of the mollusc, its feeding habits and its relation to temperature. *Aplysia* feeds on seaweed and is therefore confined to the littoral and sub-littoral zones of the land masses and islands of the world. There is some evidence that it is an annual. The eggs in vast numbers are laid in small circular capsules fastened together in long strings and deposited between tide marks (see p. 295). The free-swimming larvae proceed to open water, settling after metamorphosis in the red weed zone on the sea bottom, where they feed and grow and eventually migrate shorewards to the brown weed zone, changing colour from red to brown. They remain in shallow water on the brown weed (*Laminaria* in this country) until mature, when they migrate again to the *Fucus* zone, between tide marks. Here there may be many thousands at a time, but only for a short period. They couple in chains of from three to ten or even more, the top member of the chain acting as male only, the lowermost member as female only, and all the intermediate ones as male for the lower and female for the upper individual in the chain. After spawning, which ensues shortly after separation from coupling, many die, but it is believed that some return to deeper water. Inshore migration and spawning may occur twice in the year or only once (see Eales, 1921 : fig. 5). Thus distribution is affected by the presence of suitable weed and spawning grounds.

Approximately two-thirds of the known species inhabit tropical and sub-tropical waters, three at least (*dactylomela*, *juliana* and *parvula*) being circumglobal. Only one (*punctata*) has been recorded from within the Arctic Circle, and none is known so far from the Antarctic.

A study of the distribution of species in all the oceans suggests a division of the world into ten regions. This division does not always follow the most obvious boundaries of the oceans (Text-fig. 51).

1. North Atlantic, west, comprising the east coast of North America and Central America, Bermuda and the West Indies. *A. dactylomela*, *juliana* and *parvula* are common, particularly from Florida southwards, also *brasiliana* and *cervina*, while north of 40° north latitude *morio* and *willcoxi* reach Rhode Island and New England respectively, although *morio* also extends further south.

2. North Atlantic, north-east, consisting of the coasts of Europe and the Mediterranean. Three species are typical of this area. *A. depilans* and *fasciata* range from the Atlantic coasts of France, Spain and Portugal to become the dominant species in the Mediterranean. Although both have occasionally appeared on the British coasts, they do not extend northwards, but have spread southwards along the African coasts and the islands (see 3 below). In the north the only species is *punctata*, which reaches Greenland, Norway and the Baltic and is the only truly indigenous

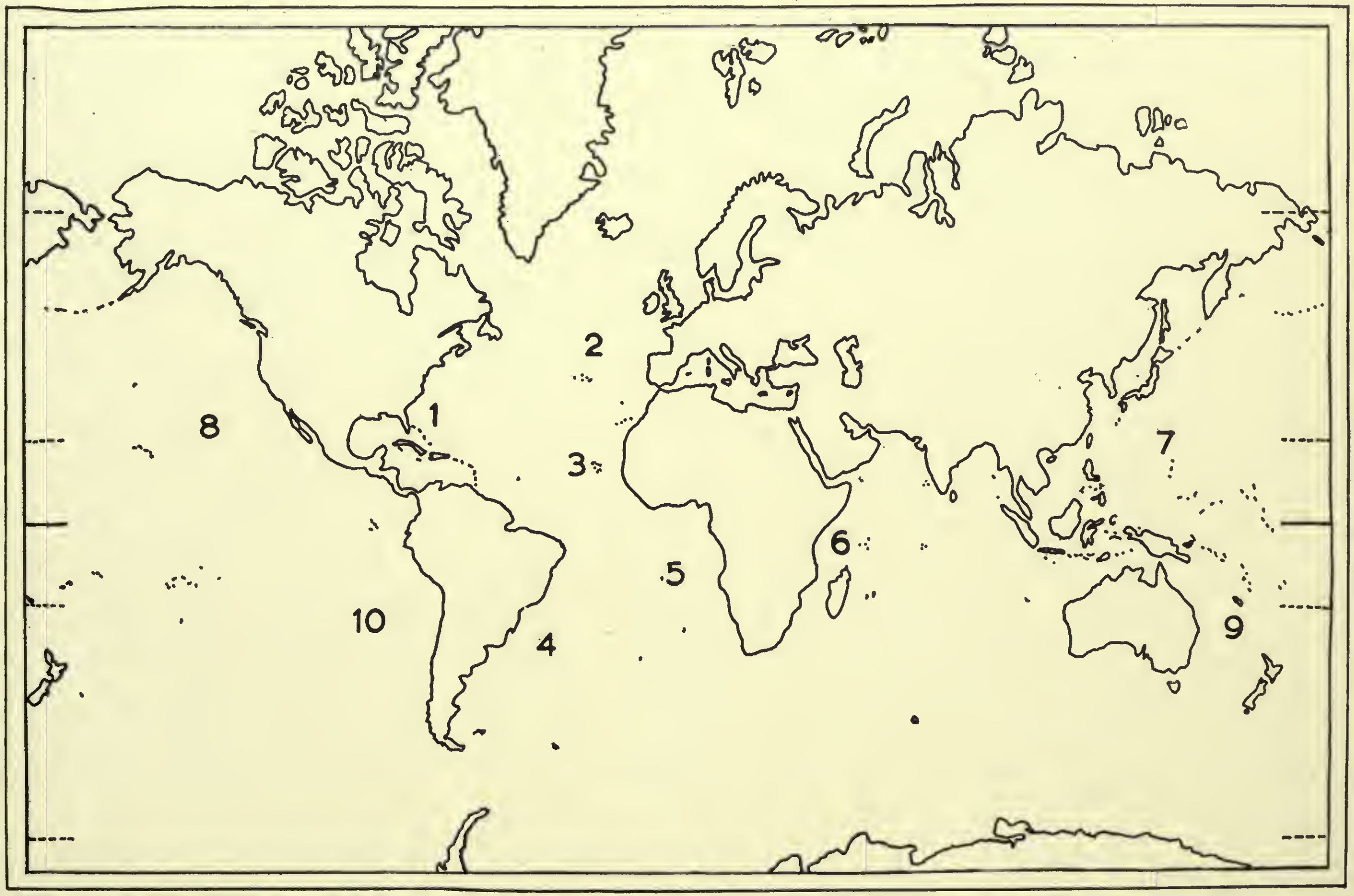

FIG. 51. Map of the world to show areas defined in the text as typical zones inhabited by the species of *Aplysia*.

British species. Southwards its range is the Mediterranean and the islands off Africa.

Recently three specimens from the Harbour of Algiers, now in the Naturhistorisches Museum in Vienna, proved to be young *juliana*, the first record of that species in this area.

3. North Atlantic, south-east, including the west coast of Africa from Morocco to the Gulf of Guinea, with the Azores, Madeira, the Canary Islands and Cape Verde Islands. *A. punctata* has been recorded from the Canaries, *depilans* from the coasts of Morocco, Rio de Oro and Madeira, and *fasciata* all down the coast to Senegal and Ghana. *A. dactylomela, juliana* and *parvula* occur both on the islands and the mainland, *brasiliana* is occasionally taken in Ghana, but *winneba* is one of the commonest species after *dactylomela*.

4. South Atlantic, west, comprising the east coasts of South America from Guiana to Cape Horn. The southern part of this area is little known, most of the records and specimens coming from Brazil. Here *brasiliana, cervina, dactylomela, juliana, nigra* and *parvula* are found, although *cervina* is typically a more northerly species.

5. South Atlantic, east, that is, the west coast of Africa from the Gulf of Guinea to the Cape, and the islands of St. Helena and Tristan da Cunha. This region also is imperfectly known. *A. brasiliana* has been found on St. Helena, *fasciata* as far south as Angola and the tough species *dura* on Tristan da Cunha. The east-west drift of ocean currents from South-west Africa towards Brazil may account for the distribution of *brasiliana*.

6. Indian Ocean, west. This extends from the Red Sea and the Persian Gulf in the north, down the east coast of Africa to the Cape, and includes the islands of the Seychelles, Mauritius, Réunion, and Madagascar, and the coasts of Pakistan, India and Ceylon. The area is rich in species and good collections have been made. The three circumglobal species *dactylomela, juliana* and *parvula* are common, the first penetrating the Red Sea from the south, while *fasciata* has reached it from the north ; *oculifera* occurs all round the coasts of the Indian Ocean, even to the west coast of Australia, but *maculata* is confined to the west, from Mauritius to South Africa. *A. cornigera* is a common species in India and Ceylon, *gracilis* inhabits the Red Sea.

7. Pacific Ocean, north-west, comprising the eastern and south-eastern coasts of Asia, Japan, Formosa, the Philippines and East Indian Islands. Again an area rich in species and inhabited by *dactylomela, juliana* and *parvula*. *A. cornigera* occurs in the Philippines and in Indo-China, *oculifera* in the East Indies, Formosa and Japan. Arthur Adams recorded a number of species from Japan, including *euchlora*, the floating species. To Baba we owe the species *kurodai* and *sagamiana* from Japan. A South Pacific species which extends northwards to the Asiatic continent is *pulmonica*.

8. North Pacific, north-east, comprising the west coast of North and Central America. Here live some of the giant members of the genus, such as *californica* of California and the Gulf, *cedrosensis*, and *rehderi* of the Gulf, alongside the ubiquitous *dactylomela, juliana* and *parvula*. The large black *vaccaria*, also of the subgenus *Aplysia*, occurs on the coast of south California, *robertsi* in Central America.

9. South Pacific, west, including the whole of Australia for convenience, Tasmania, New Zealand and Polynesia. This region has been well worked and is rich in species. The three circumglobal species are present, *juliana* exhibiting varieties of considerable range, from the small spotted *bipes* var. to larger and broader forms. In Australia in addition to *parvula, dactylomela, juliana* and *nigra* the characteristic species are *cronullae, denisoni, gigantea, reticulata, sowerbyi* and *sydneyensis*, with *oculifera* in western Australia and *extraordinaria* in the east. New Zealand has, in addition to the three world-wide species, *keraudreni*, a large and handsome species described by Rang from Polynesia, while in North Island *dura* (see Zone 5) has been found. In Polynesia the fauna of the Hawaiian Islands is best known. Again the three circumglobal species are found, and in addition *extraordinaria* and Gould's *pulmonica*.

10. South Pacific, east, comprising the west coasts of South America and the Galapagos Islands. This region is little known, most of our information being obtained from specimens collected in Peru during the early part of the nineteenth century, by d'Orbigny, Eydoux and Souleyet. *A. juliana* occurs on Galapagos and d'Orbigny's *nigra* came from Peru. His *inca* from the same coast is a valid species, but Rang's *lessoni* is probably *keraudreni*. Mazzarelli & Zuccardi's *chierchiana* is doubtful.

It will be noted that while some species have an unlimited range within the tropics and sub-tropics, others are local, even when mixed with the ubiquitous species. No explanation can be offered of this, and it is probable that more extensive collecting would extend the range of the presumed local species. On the whole, distribution of most species can be accounted for by proximity of islands to land masses, e.g. Madeira and the coast of West Africa. Currents explain the distribution of *brasiliana* at St. Helena, Ghana and in the western tropical Atlantic; and the presence of *dura* at Tristan da Cunha and New Zealand is paralleled in the distribution of fishes (see Regan, 1913). The scarcity of species on the west side of South America may be due to the steepness of the shores and depth of the water near the coast.

4. CONCLUSIONS

The subdivision of the genus into the five subgenera *Pruvotaplysia, Neaplysia, Varria, Aplysia* and *Phycophila* (see p. 271) indicates that the genus is undergoing change and radiation, from the primitive *parvula*, through the majority of the more generalized members, to the extremes in *Aplysia* and *Phycophila*. The subgenus *Neaplysia* is a small offshoot, including, it is true, very large members of a single species, but their only deviation from the main group (subgen. *Varria*) is a peculiarity of that already vestigial structure, the shell. The floating members of the subgenus *Phycophila* are little known.

The primitive characters of *Pruvotaplysia*, with its two species, *parvula* and *punctata*, are the high fusion of the parapodia posteriorly, closing in the mantle cavity behind, the large, flat, non-contractile mantle aperture, the deeply concave shell, small simple radula and the separate rounded nerve ganglia.

Varria contains about 70% of the known species, and exhibits the greatest generalization in structure, together with a wide range in distribution. In the posterior

Distribution of the Species of Aplysia *According to the Zones in Section* 3, *p.* 377

Species	Zones 1	2	3	4	5	6	7	8	9	10
brasiliana	×	..	×	×	×	..	..	..	..	..
californica	..	..	..	..	..	..	..	×	..	..
cedrosensis	..	..	..	..	..	..	..	×	..	..
cervina	×	..	..	×	..	..	..	..	..	..
cornigera	..	..	..	..	..	×	×	..	..	..
cronullae	..	..	..	..	..	..	..	..	×	..
dactylomela	×	..	×	×	..	×	×	×	×	..
denisoni	..	..	..	..	..	×	..	..	×	..
depilans	..	×	×	..	..	..	..	..	..	..
dura	..	..	..	..	×	..	..	..	×	..
euchlora	..	..	..	..	..	..	×	..	..	..
extraordinaria	..	..	..	..	..	..	..	..	×	..
fasciata	..	×	×	..	×	×	..	..	..	..
gigantea	..	..	..	..	..	..	..	..	×	..
gracilis	..	..	..	..	..	×	..	..	..	..
inca	..	..	..	..	..	..	..	..	..	×
juliana	×	×	×	×	..	×	×	×	×	×
keraudreni	..	..	..	..	..	..	..	..	×	×
kurodai	..	..	..	..	..	..	×	..	..	..
maculata	..	..	..	..	..	×	..	..	..	..
morio	×	..	..	..	..	..	..	..	..	..
nigra	..	..	..	×	..	..	..	..	×	×
oculifera	..	..	..	..	..	×	×	..	..	..
parvula	×	..	×	×	..	×	×	×	×	×
pulmonica	..	..	..	..	..	..	×	..	×	..
punctata	..	×	×	..	..	..	..	..	..	..
rehderi	..	..	..	..	..	..	..	×	..	..
reticulata	..	..	..	..	..	..	..	..	×	..
robertsi	..	..	..	..	..	..	..	×	..	..
sagamiana	..	..	..	..	..	..	×	..	..	..
sowerbyi	..	..	..	..	..	..	..	..	×	..
sydneyensis	..	..	..	..	..	..	..	..	×	..
vaccaria	..	..	..	..	..	..	..	×	..	..
willcoxi	×	..	..	..	..	..	..	..	..	..
winneba	..	..	×	..	..	..	..	..	..	..

spout of the parapodia and flexible mobile anal siphon, contractile, occasionally closed, mantle aperture, and fusion of the cerebral ganglia and the visceral pair, the subgenus links *Aplysia* with *Syphonota*.

Rang used the mantle aperture for classificatory purposes, but although in *Pruvotaplysia* and *Aplysia* it can be relied upon, in *Varria* it varies with age, state of contraction and even with individuals. Thus a young animal may possess an aperture which normally closes in the adult, an adult may show an open aperture or a closed contracted one, with or without a papilla at the point of closure. Occasionally the closed aperture may have a fringed edge. These variations make the mantle aperture unreliable for identification of the species.

In *Varria, brasiliana* resembles an enlarged, more slender and more active *cervina*, with narrower foot and more elongated head; *pulmonica* is like a plainer and flatter *dactylomela*, without rings on the skin; *winneba* resembles a smaller and broader *fasciata*, yet there appears to be no doubt that they are distinct, and their areas overlap. *A. sagamiana* is of interest because the discrete nature of its nerve ganglia recalls that of *Pruvotaplysia*, although in all other characters its relationships are with *Varria*.

The members of the subgenus *Aplysia* exhibit the greatest deviation from the characters shown by the majority of the species, and also the most marked variation within one species. The broad foot, usually with temporary formation of a posterior sucker, the absence of purple secretion but abundance of a white, milky, odoriferous substance from the simple, multiporous opaline gland, the numerous but extremely simple teeth of the radula, the spiral caecum, and the large, stout penis lying in a sheath armed with spiny warts, are peculiar to the subgenus, which contains six representatives.

In *Phycophila* the body is adapted for floating on algae; it is narrow and streamlined, with a long pointed tail resembling that of *Stylocheilus*. Unfortunately there is no information on its breeding habits; it would be interesting to know whether it comes inshore to lay its eggs, or whether the floating habit is permanent and the egg ribbons are coiled round the weed.

Aplysia is by far the largest genus in the family Aplysiidae, containing at least 35 species. *Pruvotaplysia* is more primitive than any other section of the family; *Varria* has characters which resemble those of *Syphonota* and to a lesser extent the Dolabellinae; the subgenus *Aplysia* is the most specialized and links the Aplysiinae with the Dolabriferinae and the Notarchinae because of its armed penis sheath.

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6. SPECIES REPRESENTED IN MUSEUM COLLECTIONS

A list of the species represented in the various museums is appended :

British Museum (Natural History). The complete list, with localities, is given for reference.

Aplysia brasiliana Rang, 1828

		Specimens
1856.11.21.31	No loc. Mr. Brandt's coll. Purchd.	1
1868.4.8.1	St. Helena. Pres. J. C. Mellis, Esq.	1
1869.6.5.74	Rio Janeiro Bay. 5 fms., 1867. Pres. Lords of the Admiralty (coll. Dr. Cunningham)	1
1958.1.9.1–2	Gold Coast, W. Africa. Dr. F. R. Irvine	2

Aplysia californica Cooper, 1863

1958.1.9.3–4.	Bird Rock, La Jolla, Calif., 1954. Below tide marks. Coll. Miss A. M. Clark	2
1958.1.9.170–3.	Doheny Beach State Park, Calif. 7.v.1957. From Dr. L. R. Winkler. Pres. Dr. N. B. Eales	4

Aplysia cervina Dall & Simpson, 1902

1924.11.24.4.	Pernambuco, Brazil. Pres. Eastern & Assoc. Tel. Co .	1
1958.1.9.5.	Pian Prince. Zool. Soc. coll.	1

Aplysia cornigera Sowerby, 1869

		Specimens
1958.1.9.6–10.	Ennūr (E.), 1937. Krusadai. Winckworth coll.	5

Aplysia cronullae Eales

1958.1.9.11.	Cronulla, Sydney, N.S.W. From Dr. H. Lemche. Pres. Dr. N. B. Eales *Paratype*	1
1958.1.9.12.	New South Wales. From Sydney Nat. Mus. 12083. Pres. Dr. N. B. Eales	1

Aplysia dactylomela Rang, 1828

1958.1.9.13–14.	St. Vincent, W.I. Rev. L. Guilding (re-registered from 1839.12.27.30)	2
1846.8.31.3.	Jamaica. Coll. Mr. Gosse. Purchd. Mr. Cuming	1
1868.7.4.63.	St. Vincent. Pres. Lords of the Admiralty (coll. Dr. Cunningham)	2
1876.2.5.9.	Mauritius. Purchd. Mr. Cutter	2
1876.2.5.10.	,, ,, ,, ,,	2
1890.12.28.93–4.	Shore reefs, Tonga. J. J. Lister	2
1901.7.20.17.	Kingston Harbour, Jamaica. J. E. Duerden, Esq.	1
1913.10.10.1.	Found on beach at Mosquito Bay, St. Thomas, W.I. Pres. Capt. A. Morrel	1
1927.11.2.2.	Tavinni, Fiji. Dr. H. S. Evans	1
1932.11.23.1–2.	Little Abaco, Bahamas. L. R. Crawshay	2
1954.12.10.1–3.	Schoenmaker's Kop, Easter, 1952. Pres. Dr. Wm. Macnae	3
1958..1.9.15	Anse Corail, Mahé. 22.xii.38. Winckworth coll.	1
1958.1.9.16–20.	,, ,, ,, 20.x.37. 22.xii.38. Winckworth coll.	5
1958.1.9.21–3.	Mahé, Seychelles. Winckworth coll.	3
1958.1.9.24.	S. E. Cay, Port Royal, Jamaica. 26.viii.1939. Camb. U. Jamaica Exp. 1939 (J. S. Colman)	1
1958.1.9.25.	Salt Isl., Portland, Jamaica. 13.viii.1939. Camb. U. Jamaica Exp. 1939 (J. S. Colman)	1
1958.1.9.26.	Sta. Colon 4 ? Panama Canal. Sci. Exp. Res. Ass. Pacific Cruise 1923–24. C. Crossland	1
1958.1.9.27.	St. Kitts, B.W.I. Coll. and pres. A. W. Vaughan, 1951	1
1958.1.9.28.	Takoradi, Gold Coast. Pres. Mrs. Carlyle Bell	1
1958.1.9.29–30.	Accra, Gold Coast. Irvine & Foote	2
1958.1.9.31–2.	No loc. No coll. or donor	2
1958.1.9.33.	,, ,, H. Welton, Esq.	1
1958.1.9.34–6.	,, ,, No coll. or donor	3
1958.1.9.37.	,, ,, ,, ,, ,, ,,	1
1958.1.9.186–7.	Kanai, Hawaii. Miss Alison Kay. Pres. Dr. N. B. Eales	2
1958.1.9.188.	Honolulu. ,, ,, ,, ,, ,, ,, ,, ,,	1
1958.1.9.195–199.	Pram Pram, Gold Coast. 4.ii.1950. Pres. R. Bassindale	5
1958.1.9.200.	,, ,, ,, ,, 21.xi.1949. ,, ,, ,,	1
1958.1.9.201.	,, ,, ,, ,, 17.i.1949. ,, ,, ,,	1
1958.1.9.245.	Winneba shore, Gold Coast. 22.xi.1949. Pres R. Bassindale	1
1958.10.10.2.	West Shore, St. George, Bermuda, 28.vi.1958. Coll. by Dr. R. B. Hill. Pres. Dr. N. B: Eales	1

		Specimens
1958.10.10.3–4.	Parham Sound, Antigua. Pres. Dr. J. W. Gregory	2
1958.12.30.94.	Long reef, N.S. Wales (F 19935) Victoria Nat. Mus. Melbourne, via Dr. N. B. Eales	1

Aplysia denisoni Smith, 1884

1881.11.10.11.	Port Denison, Queensland. Pres. Lords of the Admiralty (coll. Dr. Cunningham) *Holotype*	1
1881.11.10.3.	Port Molle and Port Denison, Queensland. Pres. Lords of the Admiralty (coll. Dr. Cunningham)	1
1923.1.26.6–9.	Abrolhos Isls. Pres. W. J. Dakin & C. H. O'Donoghue (Dakin's Abrolhos coll.)	4
1928.7.27.4.	Cocos Keeling Isl. Pres. Col. I. St. J. Grant	1
1958.1.9.38.	Sydney. J. B. Jukes, Esq.	1
1958.1.9.39.	No loc. ,, ,, ,, ,,	1
1958.1.9.40.	,, ,, No coll. or donor	1
1958.1.9.41.	,, ,, ,, ,, ,,	1

Aplysia depilans Linn., 1791

1845.9.26.13.	S. of Europe. Pres. P. B. Webb, Esq.	6
1848.4.27.13.	R. Tweed. Pres. Dr. G. Johnston	1
1850.6.17.12.	Weymouth Bay. Mr. Damon's coll.	1
1856.1.18.6.	Mediterranean ? Zool. Soc. coll. (sent to Soc. by Mme Jeannette Power)	1
1860.11.28.1.	R. Itchen, Southampton. Pres. J. S. Davies, Esq.	1
1866.7.30.13.	Adriatic. Purchd. L. W. Schaufuss	1
1958.1.9.165–7.	North Coast of Spain and Portugal. " Norna " Exp., 1870. Coll. Mr. Kent. Purchd. Mr. Geale (re-registered from 1872.2.3.124)	3
1898.5.21.109–10.	Zool. Stat. Naples. Norman coll.	2
1958.1.9.164.	No loc. No coll. or donor. (As *A. camelus* Cuv.)	1
1870.1.14.20.	Polperro, coast of Cornwall. Pres. J. Couch, Esq. (Holotype of *A. melanopus* Couch, 1870)	1
1958.1.9.193.	Marseilles. Peterson, Esq. (Holotype of *A. petersonii* Gray, 1828)	1

Aplysia dura Eales

1957.6.11.1.	Inshore waters Tristan da Cunha. S. Atlantic. Summer 1952. Coll. and pres. H. F. I. Elliot *Holotype*	1
1957.6.11.2.	Inshore waters Tristan da Cunha. S. Atlantic. Summer 1952. Coll. and pres. H. F. I. Elliot *Paratype*	1

Aplysia euchlora A. Adams, 1861

1860.1.18.3.	Siam. M. Mouhot's coll. (as *A. mouhoti* Gilchrist, 1895)	1

Aplysia extraordinaria Allan, 1932

1883.11.12.1–3.	Port Jackson. From N.S. Wales Coast Internat. Fisheries Exhib., 1883	3
1958.1.9.42.	No loc. No coll. or donor (old coll.)	1
1958.1.9.43.	,, ,, ,, ,, ,,	1

Aplysia fasciata Poiret, 1789

		Specimens
1958.1.9.194.	Mediterranean ? Zool. Soc. coll. (sent to Soc. by Mme Jeannette Power) (re-registered from 1856.1.18.6)	1
1958.1.9.168–9.	North coast of Spain and Portugal. " Norna " Exp. 1870. Coll. Mr. Kent. Purchd. Mr. Geale (re-registered from 1872.2.3.124)	2
1873.7.31.1.	Benguela, Africa. Purchd. Mr. Monteiro	2
1898.5.21.125.	Zool. Stat. Naples. Norman coll.	1
1908.9.22.1–2.	Las Palmas, Grand Canary. Dr. J. Cleasby Taylor	2
1958.1.9.44.	Christiansborg, Gold Coast, 9.x.36. Dr. F. R. Irvine	1
1958.1.9.45.	„ Castle rocks, Gold Coast. 12.iii.1950. Dr. F. R. Irvine	1
1958.1.9.46.	Accra, Gold Coast. Irvine & Foote	1
1958.1.9.47–8.	Arrecife, Lanzarote Isl., Canary Isls. Coll. and pres. Capt. A. K. Totton	2
1958.1.9.49.	Marseilles. Baron G. Cuvier	1
1958.1.9.252.	Chorkor shore, Accra, Gold Coast. 12.iii.1950. Pres. R. Bassindale	1
1958.1.9.253.	Trawled 4 fms., 2 miles off shore, Accra. 2.iii.49. Pres. R. Bassindale	1
1958.1.9.387–8.	St. I. Madeira. 25.iv.24. " St. George " Exp., 1924. C. Crossland	2

Aplysia gigantea Sowerby, 1869

1860.4.14.32.	Fremantle, W. Australia. Purchd. Dr. Bowerbank	1
1923.1.26.10–11.	„ „ „ Pres. W. J. Dakin & C. H. O'Donoghue (Dakin's Abrolhos coll.)	2

Aplysia gracilis Eales

1907.11.15.29.	Nr. Gemil, Lake Menzaleh, Egypt. Pres. His Excell. Min. of Education, Govt. of Egypt . . . *Holotype*	1

Aplysia juliana Q. & G., 1832

1908.9.22.3–4.	Las Palmas, Grand Canary. Dr. J. C. Taylor	2
1958.1.9.50–1.	Port Alfred, South Africa. 8.iii.1955. Pres. Dr. Wm. Macnae	2
1958.1.9.52–3.	Hermanus, Cape of Good Hope. Jan. 1949. Pres. Dr. Wm. Macnae	2
1958.1.9.54–9.	Arrecife, Lanzarote Isl., Canary Isls. Mar.–May 1955. Coll. and pres. Capt. A. K. Totton	6
1958.1.9.60–7.	St. I. Madeira. 28.iv.1924. " St. George " Exped., 1924	8
1958.1.9.68.	Galapagos. C. Crossland coll. 1923–24.	1
1958.1.9.69.	Port Phillip, Victoria, Australia. J. B. Wilson coll. (has dried up at some time)	1
1958.1.9.177.	Fishers Isl., New York. Jan. 1950. Coll. H. L. Ferguson. Pres. Dr. N. B. Eales	1
1958.1.9.178–9.	Tomioka, Amakusa, Japan. Pres. Dr. N. B. Eales	2
1958.1.9.180.	„ „ „ „ „ „ „ „	1
1958.1.9.190.	Keelung, Taiwan (Formosa). Mr. I. Callan. Pres. Dr. N. B. Eales	1

		Specimens
1958.1.9.246.	Gold Coast, Africa. Pres. R. Bassindale	1
1958.1.9.389–92.	St. I. Madeira. 25.iv.24. "St. George" Exped., 1924. C. Crossland	4
1958.12.30.95.	Long Reef, N.S. Wales (F19934) Victoria Nat. Mus., Melbourne, via Dr. N. B. Eales	1
1958.12.30.96.	Portland Bay, N.S. Wales (F18980) Victoria Nat. Mus., Melbourne, via Dr. N. B. Eales	1

Aplysia juliana var. *bipes* Pease, 1860

1958.1.9.70–9.	Newcastle, N. H. [New South Wales]. Rev. C. P. N. Wilton	14
1958.1.9.80.	Peru. Rev. W. Hennah	1
1958.1.9.81–5.	Fort Jesus, Mombasa. 27–30.x.1952. Pres. L. F. Brown	5 +egg-mass
1958.1.9.86–91.	Diamond Head Reef Flat, Oahu, Hawaii. 23.xi.1956. Pres. Dr. N. B. Eales	6

Aplysia juliana var. *quoyana* Engles & Eales, 1957

1881.10.6.55.	Port Jackson. Pres. Admiralty. Dr. Coppinger, H.M.S. "Alert". *Holotype*	1
1883.11.12.4–5.	Port Jackson. From Internat. Fisheries Exhib., 1883	2
1887.12.22.1–6.	Hakodadi, Japan. Pres. Rev. W. Andrews	8
1921.12.20.291–2.	Misaki, Japan. A. V. Insole	2
1958.1.9.95.	Port Jackson. J. B. Jukes (1845)	1

Aplysia juliana var. *sibogae* Bergh, 1905

1883.4.25.19.	Kurrachee. Exch. with Kurrachee Mus.	1
1958.1.9.181.	Tomioka, Amakusa, Japan. Pres. Dr. N. B. Eales	1

Aplysia keraudreni Rang, 1828

1958.1.9.96–7.	Channel N. of Quarantine Isl., Otago Harbour. + 2 fms. 18″ dredge. From Portobello Mar. Biol. Sta., Otago Harbour, New Zealand. Pres. Dr. N. B. Eales	2

Aplysia kurodai Baba, 1937

1921.12.20.293–6.	Misaki, Japan. A. V. Insole	4
1958.1.9.184–5.	Tomioka, Amakusa, Japan. Pres. Dr. N. B. Eales	2

Aplysia maculata Rang, 1828

1954.12.10.14–17.	Hermanus, Cape Province. Jan. 1949. Pres. Dr. Wm. Macnae	4
1958.1.9.102–6.	Hermanus, Cape Province. Jan. 1949. Pres. Dr. Wm. Macnae	5

Aplysia morio Verrill, 1901

1958.1.9.107.	Florida. U.S. Nat. Mus. Pres. Dr. N. B. Eales	1
1958.10.10.1.	Ferry Reach, St. George's West, Bermuda. June 1958. Coll. by Dr. R. B. Hill. Pres. Dr. N. B. Eales	1

Aplysia nigra d'Orbigny, 1837

		Specimens
1886.6.3.61.	Port Jackson. Purchd. Dr. von Lendenfeld	1
1958.1.9.93.	No loc. Haslar coll. J. O. Goodsir	1
1958.1.9.94.	New South Wales	1
1958.12.30.97–9.	Drummoyne, N.S. Wales (F19931). Victoria Nat. Mus., Melbourne, via Dr. N. B. Eales	3

Aplysia nigra var. *brunnea* Hutton, 1875

1886.11.18.3.	Dunedin, New Zealand. Purchd. Comm. for New Zealand, India and Colon. Exhib., 1886	1

Aplysia nigra var. *delli* Eales

1958.1.9.92.	North Isl., New Zealand. From Wellington Mus. Pres. Dr. N. B. Eales . . . . . . *Holotype*	1

Aplysia oculifera Ad. & Rve., 1850

1869.7.8.35.	Red Sea, Gulf of Suez. R. McAndrew	2
1883.4.25.20.	Kurrachee. Exch. with Kurrachee Mus.	1
1954.12.10.13.	Flat rocks beyond Hotel Pollock, Port Elizabeth. Pres. Dr. Wm. Macnae	1
1958.1.9.108.	Abu Zabad, on reef at low tide, Aqaba. 11.ii.1949. Coll. N. B. Marshall	1
1958.1.9.109–13.	Bokness, Alexandria Div., S. Africa. Mar. 1954. Pres. Dr. Wm. Macnae	5
1958.1.9.114.	Trincomali. 16.iii.38. Winckworth coll.	1
1958.1.9.191–2.	Reef N. Ngatpaet Passage, E. Babethuap, Palau Isls. Ostheimer ? Sta. 425. Pres. Acad. Nat. Sci. Philad. (Tucker Abbott)	2

Aplysia parvula (Guilding MS.) Mörch, 1863

1958.1.9.115–16.	St. Vincent, W.I. Purchd. Rev. L. Guilding's sale (re-registered from 1839.12.27.30)	2
1877.4.16.14.	S. Africa. Sent by Dr. Daniel Hahn	1
1954.12.10.4–12.	Flat rocks beyond Hotel Pollock, Port Elizabeth. Pres. Dr. Wm. Macnae	21
1954.12.10.18–27.	Rocks at Kariega mouth, C. of Good Hope. Pres. Dr. Wm. Macnae	29
1958.1.9.117–18.	W. Indies. No donor or coll.	2
1958.1.9.119–20.	No loc. ,, ,, ,, ,,	2
1958.1.9.121–30.	New South Wales. Godwin-Austen coll.	14
1958.1.9.134–40.	Miller's Point, Cape Peninsula, S. Africa. Dec. 1949. Pres. Dr. Wm. Macnae	7 +egg-mass
1958.1.9.131–33.	Berbera, Brit. Somaliland. Feb. 1949. Pres. A. Fraser Brunner	3
1958.1.9.182–3.	Tomioka, Amakusa, Japan. Pres. Dr. N. B. Eales	2
1919.10.7.55.	S. Cheval Paar, Ceylon. Coll. Prof. Herdman, 1902. Pres. T. J. Evans (Holotype of *A. intermedia* Farran, 1905)	1
1958.12.30.100–1.	Portland, Victoria (F18981) Victoria Nat. Mus., Melbourne, via Dr. N. B. Eales	2

Aplysia pulmonica Gould, 1852

		Specimens
1848.4.3.13.	Norfolk Isl. Sir J. Richardson	1
1877.1.15.16.	Samoa Isl. Pres. Rev. S. J. Whitmee	2
1958.1.9.141–2.	Anini, Kauai, Hawaii. 31.xii.1956. Pres. Dr. N. B. Eales	2
1958.1.9.143.	Port Molle. J. B. Jukes	1
1958.1.9.144.	Port Jackson. J. B. Jukes	1

Aplysia pulmonica var. *tryoniana* Pilsbry, 1895

1958.1.9.145.	No loc. J. B. Jukes (1845)	1

Aplysia punctata Cuvier, 1803

1851.7.4.4.	? Tynemouth. Pres. Slater	1
1858.5.28.5.	Guernsey. Purchd. Mr. Joshua Alder	5 +spawn
1862.10.27.33.	Bohuslan, Sweden. A. W. Malm, No. 66	1
1865.2.11.16.	Scotland. W. Carruthers, Esq.	1
1866.12.31.5.	Taken in crab pots 20 fms., Polperro, Cornwall. Purchd. Laughrin	4
1868.3.6.62.	? Europe. Purchd. of Damon	1
1872.2.3.164.	N. coast of Spain and Portugal. "Norna" Exp. 1870. Coll. Mr. Kent. Purchd. Mr. Geale	1
1888.12.3.8–10.	Firth of Lorn. 17–30 fms. J. Murray	3
1898.5.21.111–13.	Zool. Stat. Naples. Norman coll.	3
1927.2.24.2–3.	Kames Bay, Cumbrae. Mrs. Stebbing	2
1927.2.24.4–5.	Ilfracombe. Mrs. Stebbing	2
1931.6.23.8–9.	,, ? donor	2
1946.7.27.1.	Selsey Bill. Pres. E. Heron-Allen	1
1947.6.12.1.	Plymouth Sound, 1946. Purchd. Mar. Biol. Ass. Plymouth	1
1947.6.12.7.	Yealm Estuary, Devon. Purchd. Mar. Biol. Ass. Plymouth. Coll. W. J. Rees, 8.iv.1947.	1
1948.7.10.1.	Ceibach Beach, Newquay, Cardiganshire, Wales. Pres. Wm. D. Evans	1
1958.1.9.146–7.	Marseilles. G. Cuvier	2
1958.1.9.148–9.	Sardinia. Prof. Bonelli	2
1958.1.9.150.	Devon. G. Montague	1
1958.1.9.151.	Torbay. Mrs. Griffiths	1
1958.1.9.152–3.	Probably British. No donor or coll.	2
1958.1.9.154–7.	No loc. ,, ,, ,, ,,	4
1958.1.9.158.	,, ,, ,, ,, ,, ,,	1
1958.1.9.159–60.	Aberdaron Bay, N. Wales, 15–20 fms. 27.vii.1936. Coll. D. D. John & F. C. Fraser	2

Aplysia reticulata Eales

1886.2.22.29.	N.W. Australia. Purchd. Capt. Beckett. *Holotype*	1
1887.5.12.3.	Dampier Archipelago, N.W. Australia. Purchd. Capt. Beckett	1

Aplysia robertsi Pilsbry, 1895

1958.1.9.161.	N. coast, Central America. Pres. Capt. Dow	1

Aplysia sowerbyi Pilsbry, 1895

		Specimens
1958.1.9.189.	Long Reef, Sydney, N.S.W. E. Pope and party. Pres. Dr. N. B. Eales	1
1958.12.30.102–4.	Western Port, Victoria (F18984) Victoria Nat. Mus. Melbourne, via Dr. N. B. Eales	3

Aplysia sydneyensis Sowerby, 1869

1883.11.12.6.	Port Jackson. N. S. Wales Coast Internat. Fisheries Exhib. 1883	1

Aplysia vaccaria Winkler, 1955

1958.1.9.174.	Doheny Beach State Park, 2 m. SW. San Juan Capistrano, Calif. 15.v.1957. From Dr. L. R. Winkler. Pres. Dr. N. B. Eales	1
1958.1.9.175.	Digestive gland and penis. From Dr. L. R. Winkler. Pres. Dr. N. B. Eales	1

Aplysia willcoxi Heilprin, 1886

1934.9.11.4.	Dry Tortugas. G. Tandy & J. S. Colman	1
1958.1.9.176.	Fishers Isl., New York. Jan. 1950. Coll. H. L. Ferguson. Pres. Dr. N. B. Eales	1

Aplysia winneba Eales, 1957

1957.5.14.1.	Chorkor, Accra, Gold Coast. 14.x.1949. Pres. R. Bassindale *Lectotype*	1
1957.5.14.2.	Chorkor, Accra, Gold Coast. 14.x.1949. Pres. R. Bassindale *Paratype (figured)*	1
1957.5.14.3.	Chorkor, Accra, Gold Coast. 14.x.1949. Pres. R. Bassindale *Paratype*	1
1957.6.18.1.	Nr. Dixcove, Gold Coast. Pres. Miss V. J. Foote *Paratype*	1
1957.6.18.2–3.	Pram Pram, Gold Coast. Aug. 1939. Pres. Miss V. J. Foote *Paratypes*	2
1957.6.18.4–7.	Christiansborg, nr. Accra, Gold Coast. Pres. Miss V. J. Foote *Paratypes*	4
1957.6.18.8.	Accra, Gold Coast. Pres. Dr. F. R. Irvine & Miss V. J. Foote *Paratype*	1
1882.8.16.17–18.	Gold Coast. Pres. Maj. Burton & Capt. Cameron *Paratypes*	2
1958.1.9.162.	Takoradi, Gold Coast. Pres. Mrs. Carlyle Bell	1
1958.1.9.163.	Santiago Isl., C. Verde. 23.iv.1939. Pres. C. R. Stoner	1
1958.1.9.202–11.	Pram Pram, Gold Coast. 4.ii.50. Pres. R. Bassindale *Paratypes*	14
1958.1.9.212.	Pram Pram, Gold Coast. 4.ii.50. Pres. R. Bassindale *Paratype*	1
1958.1.9.213–19.	Pram Pram, Gold Coast. 21.xi.49. Pres. R. Bassindale *Paratypes*	7
1958.1.9.220–7.	Winneba shore, Gold Coast. 15.xi.49. Pres. R. Bassindale *Paratypes*	8

		Specimens
1958.1.9.228.	Axim Hospital Reef, Accra, Gold Coast. 13.iv.49. Pres. R. Bassindale . . . . *Paratype*	1
1958.1.9.229–30.	Chorkor, Gold Coast. March 1949. Pres. R. Bassindale *Paratypes*	2
1958.1.9.231–6.	Dredge haul No. 2, Gold Coast. 4.i.51. Pres. R. Bassindale . . . . *Paratypes*	6
1958.1.9.237–40.	Christiansborg, Gold Coast. 15.i.49 and 17.iii.49. Pres. R. Bassindale . . . . *Paratypes*	4
1958.1.9.241–4.	Dixcove shore, Gold Coast. 7.ii.51. Pres. R. Bassindale *Paratypes*	4
1958.1.9.247–50.	Gold Coast. Pres. R. Bassindale . . . . *Paratypes*	4
1958.1.9.251.	Chorkor shore, Gold Coast. 12.iii.50. Pres. R. Bassindale . . . . *Paratype*	1

Types of nominal species not now included in the genus *Aplysia* :

Syphonota geographica Ad. & Rve.

1882.2.23.574–5.	Thursday Isl., Torres Straits, 4–5 fms. H.M.S. " Alert ". Coll. Dr. Coppinger. (Holotype and Paratype of *A. piperata* Smith, 1884.)
1882.2.23.571–3.	Thursday Isl., Torres Straits, 4–5 fms. H.M.S. " Alert ". Coll. Dr. Coppinger. (Holotype and 2 Paratypes of *A. sparsinotata* Smith, 1884.)
1860.1.18.2.	Siam. M. Mouhot's coll. (Holotype of *A. Mouhoti* Gilchrist, 1895)

Australian Museum, Sydney, New South Wales : *dactylomela, extraordinaria* (holotype), *juliana, nigra, parvula, reticulata, sydneyensis, sowerbyi.*

Australia, National Museum of Victoria, Melbourne : *dactylomela, extraordinaria, juliana, oculifera, parvula, sydneyensis.*

New Zealand, Christ Church Museum, Otago and Portobello Marine Biological Station : *juliana, keraudreni, nigra, parvula.*

New Zealand, Dominion Museum, Wellington : *dura, juliana, nigra, keraudreni, parvula.*

United States National Museum (the Smithsonian Institution), Washington, D.C., U.S.A. : *brasiliana, californica, cedrosensis* (holotype), *cervina, dactylomela, juliana, morio, parvula, pulmonica, punctata, rehderi* (holotype), *willcoxi.*

Philadelphia, Academy of Natural Sciences : *brasiliana, californica, cervina, dactylomela, depilans, juliana, oculifera, parvula, punctata, robertsi, willcoxi.*

Stockholm, Naturhistoriska Riksmuseum : *brasiliana, californica, cervina, dactylomela, depilans, morio, parvula, pulmonica, sagamiana.*

København Universitets Zoologiske Museum : *brasiliana, cervina, cornigera, cronullae* (type), *dactylomela, fasciata, gigantea* (shell), *juliana, keraudreni, morio, oculifera, parvula, pulmonica, punctata, sydneyensis.*

Paris, Muséum National d'Histoire Naturelle : *brasiliana, californica, cervina, cornigera, dactylomela, depilans, extraordinaria, fasciata, inca* (type), *juliana, kurodai, maculata, oculifera, parvula, pulmonica, punctata.*

Wien, Naturhistorische Museum : *brasiliana, californica* (shells), *dactylomela, fasciata, juliana, kurodai, morio, oculifera, parvula, sydneyensis.*

7. REFERENCE LETTERS

abd.ao.—abdominal aorta.
an.—anus.
ant. giz.—anterior portion of gizzard.
ant. giz. t.—anterior gizzard tooth.
an. s.—anal siphon.
an. si.—anal sinus in shell.
apex.—apex of the shell.

b. pl.—basal plate of tooth.
bl.—blade of tooth.

caec.—caecum.
calc.—calcareous portion of shell.
ceph. t.—cephalic tentacle.
ct.—ctenidium.
cu.—cusp of tooth.

d.—denticle of tooth.

e.—eye.

f.—foot.

g. buc.—buccal ganglion.
g. c.—cerebral ganglion.
g. par.—parietal ganglion.
g. ped. pedal ganglion.
g. pl.—pleural ganglion.
g. v.—visceral ganglion.
gen. ap.—genital aperture.
gl. herm. hermaphrodite gland.

haem.—haemocoele.
hd.—head of tooth.

int.—intestine.

l. ped. m.—longitudinal pedal muscle.
l. pl. visc. conn.—left pleuro-visceral connective.
la. herm. d.—large hermaphrodite duct.
lat.—lateral tooth.
liv.—digestive gland.

mant.—mantle.
mant. ap.—mantle aperture.
mant. cav.—mantle cavity.
mant. f.—fold of mantle beginning to envelope the shell.

op. gl.—opaline gland.
op. gl. ap.—aperture of opaline gland.

p. giz.—posterior portion of gizzard.
p. gl.—purple gland.

pap.—papilla on mantle.
para.—parapodium.
para. sin.—parapodial sinus.
pc.—pericardium.
ped. a.—pedal artery.
ped. gl.—pedal gland.
ped. lac.—pedal lacuna.
ped. n. 3.—third pedal nerve.
ped. su.—pedal sucker.
pn.—penis.
pn. s.—penis sheath.
pz.—sensory (brush) cell.

R.—rhachidian tooth.
r. bd.—right bile duct.
r. pl. visc. conn.—right pleuro-visceral connective.
rec.—recurved border of shell.
ren. p.—renal pore.
ren. s.—renal sac (kidney).
ret. mant.—retractor muscle of visceral hump.
ret. pn.—retractor penis muscle.
rh.—rhinophore.

sem. gr.—seminal groove.
sh.—shell.
sh. f.—shell-forming region of the mantle.
stom.—stomach.

t.—tail.

8. LITERATURE

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[1] This is a fossil shell, which is not an *Aplysia*. Depontaillier (1880) says Philippi's specimens are only the linings of the shells of *Pectunculus* and *Lucina*.

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